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Importance of Isolation to
Eastern Chipmunk (Tamias striatus)
Populations: Island Analogs in
an Agricultural Mosaic

by

Malcolm T. Henderson, B.Sc.

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

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May, 1981

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ABSTRACT

Small natural populations of the eastern chipmunk (Tamias striatus) occurring in 4 square kilometers of patchy agricultural habitat including 5 woodlots and surrounding fencerows were studied near Ottawa, Canada. Small woodlot populations were at risk of extinction from natural processes. Following natural and experimental extinctions, recolonization was rapid. Fencerows served as corridors facilitating movement but woodlots were not absolutely isolated if separated by a distance of 0.5 km of grassy field.

In fencerows, chipmunks selected areas having more rocks, rails, a more open shrub layer and a particular set of plant species. Overwintering and breeding were found to occur in some stretches. In woodlots, analysis of drainage conditions surrounding burrows showed selection for sites further from vernal ponds and more commonly on mounds.

The MacArthur-Wilson theory of island biogeography did not provide a useful conceptual model for understanding chipmunk populations in these patchy habitats.

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INTRODUCTION

The use of theory derived from the study of island biogeography to understand the ecology of small populations occupying insular habitats on continents has gained general acceptance since the publication of the seminal paper by MacArthur and Wilson (1967). These authors suggested that small farm woodlots should conform to the definition of an island as a fragment of isolated habitat, permitting the application of this body of theory to such examples. In fact many different habitats on continents should have the requisite isolation and small area to permit the application of this theory (Simberloff 1974) and it has often been noticed that habitats on continents are not continuous but arranged as disjunct patches varying in suitability and isolation. Certainly isolation can have an important influence on the ecology of species, depending on the dispersion of the patches and the mobility of the organisms across intervening habitat types. A considerable number of studies have addressed the functioning of the more isolated patches in island biogeographical terms. To cite specific cases, the theory has been applied to the distribution of weeds in vacant lots (Crowe 1979), parasites of host plants or animals (Dritschilo et al. 1975, Freeland 1979, Lawton and Price 1979, Janzen 1973), aquatic species in lakes (Aho 1978a,

1978b, Barbour and Brown 1974), plant species in vernal pools (Holland and Jain 1981, Rosario 1979), and cave dwelling invertebrates (Culver et al. 1973, Vuilleumier 1973). Such studies have been of considerable value in elucidating population processes in small units of habitat (Barbour and Brown 1974, Daugherty et al. 1978, Gliwicz 1980, Heliwell 1976, Janzen 1973, Simberloff and Wilson 1969, Tamarin 1977). The generality of isolation between habitats makes the island biogeographic theory potentially useful over a tremendous range of habitats because much of the biotic world is arranged as a series of discontinuous patches (Simberloff 1974).

Understandably, for a body of theory with such broad implications for ecology, many corrections and additions have been made since its appearance in 1967 (Brown and Kodric-Brown 1977, Diamond 1975b, Henbry and Cairns 1980, Simberloff 1978). However, the rather uncritical use of this theory in many situations in which its basic tenets are improperly substantiated and often merely assumed by the investigator has drawn sharp criticism (Gilbert 1980). In particular, no demonstration that continental areas considered as "islands" are in fact isolated from one another (Culver et al. 1973, Dritschilo et al. 1975, Gottfried 1979, Vuilleumier 1973) may lead to the use of this theory in inappropriate circumstances. The direct relationship between island area and species number

postulated by the theory arises from the occurrence of an equilibrium between opposing forces of immigration and stochastic extinction among small island populations. Thus a change in species composition, or turnover, would occur with time. A demonstration of turnover would be strong evidence for an equilibrium situation although unequivocal evidence of this has been difficult to obtain (Aho 1978b, Daugherty et al. 1978, Diamond 1969, Gilbert 1980, Simberloff 1970). Particular qualifications of the theory, with respect to the notion that a single area of maximal size will contain a maximal number of species has sparked heated controversy as well (Diamond 1976, Simberloff and Cole 1976a, 1976b, Whitcomb et al. 1976).

The present study was undertaken to examine the applicability and usefulness of the MacArthur-Wilson theory of island biogeography to the populations of eastern chipmunks (Tamias striatus) in small farm woodlots in eastern Ontario. This species is commonly regarded as a woodland dweller although it penetrates brushy fencerows (Wegner 1976). Little is known of the natural history of the species in this environment as virtually all research has been undertaken in the chipmunk's usual deciduous forest habitat. It is essential to determine this animal's ability to travel between woodlots and to recolonize habitats which lack a population to demonstrate that the woodlots function as "islands" in a biogeographic

sense.

STUDY AREA

Five woodlots with surrounding fencerows 38 km south of Ottawa, Ontario in Osgoode township, municipality of Ottawa-Carleton were studied. The area covered lots 35 to 40 in concessions 3 to 5. Latitude and longitude at the center of the area was 45° 8' 30" N and 75° 31' E. The land had little relief, ranging from an elevation of 76 m asl in the vicinity of the South Castor River in the center of the area to 84 m asl on a low hilltop to the north of the largest woodlot. The soil was predominately Carp clay loam with Grenville loam forming a low hill in the north-eastern part as well as a small area in the south-west (Hills, et al, 1944). The woodlots have been numbered from 1-5 as shown in Fig.1.

Woodlot No. 1.

This woodlot was on very flat ground and had considerable pooling of water in shallow depressions following snowmelt in the spring, the pools remaining until June. The vegetation was predominately basswood (Tilia americana), red maple (Acer rubrum), white ash (Fraxinus americana), and beech (Fagus grandifolia), although there was a clump of hemlock (Tsuga canadensis) and balsam fir (Abies balsamea) on a knoll near the north-west corner. See Appendix 1 for a more complete list

Figure 1.

Woodlots and fencerows trapped in 1979-1980.

of species. Since 1978 the owner, Mr. Jack McDairmid had been selectively removing dead elm and any large trees of all species which appeared senescent as well as straight mature ash for saw logs. Prickly ash (Zanthoxylum americanum) was patchily distributed in the understory, becoming dense near the east side. In the absence of prickly ash, the shrub layer was little developed, and was especially open under the hemlock and fir. The major herbs were Virginia waterleaf (Hydrophyllum virginianum), ostrich fern (Matteuccia struthiopteris) and spotted touch-me-not (Impatiens capensis). The touch-me-not grew densely in areas disturbed by the logging activities of Mr. McDairmid.

Woodlot No.2.

More abundant Carex spp. indicated that this woodlot was somewhat more poorly drained than wood 1. Also smooth horsetail (Equisetum laevigatum) survived well in some of the moister areas. Species of trees present were similar to wood 1 (Appendix 1), with the exception that hemlock and fir were absent. Prickly ash grew densely in parts of the understory, particularly along the northern and western edge. Poison ivy (Rhus radicans) formed a dense carpet in parts of the herb layer. The presence of large well-rotted stumps indicated some logging activity in past years. The wood had remained totally unused in recent

times, however. A region of poorly drained ground along the northeastern side had produced a dense second growth of red maple.

Woodlot No. 3.

This was by far the largest wood and also was on flat land with imperfect drainage. A 1.5 m deep ditch ran through the woods from the center of the north side to the south-west corner and emptied into the South Castor River. It facilitated spring runoff but otherwise had no current. Water still pooled on the ground following snowmelt and the puddles occasionally lasted until June. The vegetation was similar to wood 1 with somewhat more sugar maple and bitternut hickory (Carya cordiformis). Selective cutting had been carried out here as well, again in the distant past as the stumps were rotten. Prickly ash was abundant in the understory, especially in the western half and near the southern edge. The presence of this shrub in the understory of a wood is unusual and suggests that it became firmly established when the canopy was open. Much of the prickly ash here was in excess of 5 m tall. I suspect that after natural closure of holes in the canopy, the prickly ash will not be able to survive in the understory. The herb layer was dominated by ostrich fern and Virginia waterleaf as in wood 1. Dairy cattle used this woodlot (mostly for shade as there was little

grazing) from mid-July of both summers onward and obliterated most of the herb layer, except in the extensive areas of prickly ash.

Woodlot No. 4.

This woodlot was the most poorly drained of the five. Water collecting in the south-west corner remained long enough to allow the growth of rank marsh vegetation (Carex and Scirpus spp.). However, by midsummer of both years the area was dry. The vegetation of the woodlot consisted largely of second growth species which had established following a clearcut in the 1930's. Most trees were small (15 cm dbh or less) although some very large, old red maples remained. Common species were basswood, burr oak (Quercus macrocarpa), red maple and aspen poplar (Populus tremuloides). Prickly ash was abundant in the understory. Willow and meadowsweet were very common in the open and rather ragged edges to the east and south.

Woodlot No. 5.

This woodlot was imperfectly drained in the southern and western parts similar to woods 1 to 3. The undulating terrain produced patches of poor drainage interspersed with better drained areas. As a whole this area supported basswood, white and black ash (Fraxinus americana and F.

nigra), red maple and ironwood (Ostrya virginiana). The northern and eastern half contained vegetation more typical of mesic woodland such as sugar maple, bitternut hickory and beech in addition to the above. The understory contained little prickly ash. Where the canopy was more open Virginia creeper (Parthenocissus quinquefolia) and moonseed (Menispermum canadense) were common. The herb layer was largely lady fern (Athyrium filix-femina), spinulose wood fern (Dryopteris spinulosa) as well as ostrich fern (Matteuccia struthiopteris) in the moister parts. White snakeroot (Eupatorium rugosum) was common in any disturbed areas. Also Virginia waterleaf and poison ivy were common over large areas of the herb layer. Some selective cutting was indicated by rotting piles of cordwood.

Fencerows

All fencerows in the study area were the result of neglect of a strip of land along a fenceline between adjacent fields. piled rocks, fallen rails from no-longer-functional rail fences and considerable quantities of prickly ash added to the three-dimensional structure and often contributed to the width. The presence of large mature trees in many of the fencerows attested to their considerable age. The natural invasion and growth of species has resulted in an association

possessing a great deal of heterogeneity in structure, width and species composition along the length of any particular fencerow. Plant species present are listed in a later section (Table 9).

In summary, the woodlots were all on flat clay loam and remained moist for periods in the spring, probably accounting for the relative scarcity of sugar maple and other mesic woodland species. Recent human activity or disturbance was slight, except for grazing in wood 3 and the selective cutting in wood 1.

MATERIALS AND METHODS

Trapping was done in all woodlots and surrounding fencerows in the summers of 1979 and 1980 (see Appendix II for trapping schedule). Sherman-type live traps (7.5 by 7.5 by 30.5 cm manufactured by Canadian Penitentiary Industries) were baited with sunflower seeds and a mixture of peanut butter and oatmeal. All traps were provided with terylene fiberfill batting for insulation.

The traps were set out on a 20 m grid in each woodlot and at 20 m intervals along fencerows. All trap locations were flagged with numbered plastic tape so that trap locations were identical in all succeeding trapping periods. Tables 1 and 2 show numbers of traps and trap days in woodlots and fencerows. Traplines were set along the fencerows in the vicinity of wood 3 in 1979. In 1980 the trapping program in the fencerows was expanded. Additional fencerows trapped were those numbered 10, 11 and 12 (Fig. 1) in the vicinity of wood 3 and 13, and 14 and 15 in the vicinity of wood 1 and 2. This was possible due to an increase in number of traps available for use on this project, from 120 in 1979 to 220 in 1980. In total, 787 trapping locations were used in 1979 and 870 in 1980.

Each trap was set at a given trap location on one day, then checked on the four following days. On the fourth day the traps were moved elsewhere.

Table 1.

Woodlots used in 1979-80

	Size (ha)	No. of trapping locations	Trap days	
			1979	1980
Wood 1	5.1	110	880	1760
Wood 2	2.9	75	600	1200
Wood 3	8.9	247	1976	3952
Wood 4	4.6	104	832	1664
Wood 5	5.1	111	888	1776
Total			5176	10352

Table 2.

Fencerows trapped in 1979 and/or 1980.

Fencerow	Nearest Wood	Length (m)	No. of traps	Years trapped	Trap days 1979	Trap days 1980
1	Wood 3	180	9	both	72	144
2	"	500	25	"	200	400
3	"	160	8	"	64	128
4*	"	280	14	"	112	224
5	"	160	8	"	64	128
6	"	280	14	"	112	224
7	"	160	8	"	64	128
8	"	180	9	"	72	144
9*	"	120	6	"	48	96
10	"	160	8	1980		128
11	"	400	20	1980		320
12	"	500	25	1980		400
13	Wood 1	620	31	1980		496
14	"	200	10	1980		160
15	Wood 2	480	24	1980		384
Total					808	3504

* completely cut by landowners in late summer 1980

On capture each chipmunk was dumped into a plastic mesh bag for handling; unmarked chipmunks were tagged with a metal tag in each ear (MSPT Monel size 20101, Gey Band and Tag Co. Box 363, Norristown, Pa. 19404) The ear tag numbers and weights (g) of animals were recorded as well as the the trap location, date, sex and reproductive condition. If no evidence of recent breeding was observed, the animal was classed as "inactive"; for females, evidence of lactation at the time of capture or in the recent past was recorded as well as any swelling of the vulva indicative of estrus and breeding (Smith and Smith 1975). For males, any darkening or enlargement of the scrotum indicating that the animal was in breeding condition was recorded. Females were recorded as breeding in either spring or summer, since they can potentially breed twice a year. Since no observations of males were made prior to their breeding in spring, any reproductively active males were recorded as breeding in summer. Any unmarked nonreproductive animals could be definitively called "young of the year" if they were less than 75 g when caught (Smith and Smith 1972). Since the young animals grow rapidly and exceed this weight at 10-11 weeks of age (Smith and Smith 1972) any individuals caught at weights greater than 75 g were called "uncertain age" animals. Besides large young, this category may contain some subadults and adults which were not reproductively

active.

To test the ability of animals to reach or recolonize habitats, all animals were removed from woodlots 1 and 2 in 1980 by trapping from May 15 to May 27 in wood 1 and from May 17 to May 27 in wood 2. Four days of unsuccessful trapping following the last chipmunk capture was considered sufficient indication that removal was complete. Trapped animals were released in a woodlot approximately 4 km west of the point of capture. Subsequent arrival of immigrants was recorded by trapping in 4-day trapping periods as described above.

All trapping fatalities were deposited with the Carleton University Museum of Zoology.

To discern the inhabitable proportion of each woodlot and to assess the habitats for "quality", the distribution of chipmunk burrows was compared to various aspects of woodlot soil moisture conditions. The active burrows in wood 1 were mapped between 29 February and 24 April 1980. Nearly all snow had melted by 29 March 1980. Prior to snowmelt, I followed tracks to burrows which I flagged with plastic tape. After 29 March observations of active chipmunks revealed more burrows and confirmed that previously flagged burrows were active. Since it was impossible to tell whether burrows were connected by tunnels below ground, any burrow more than 5 m away from another was recorded as a separate burrow.

On 22 April 1980, at each burrow entrance I recorded the distance to the nearest standing water, local topography (whether the burrow was on a mound or depression or neither) and the depth to the frost line. A soil sample of known volume (45 cm³) was taken to determine percent water content by volume. These values were compared to samples taken at an equal number of randomly located points in the woodlot. These points were selected by taking random distances vertically and horizontally on a map grid and locating these points in the woodlot. Any randomly located points falling in areas of standing water were removed from consideration. The soil samples were collected by pressing a short segment of pipe into the wall of a soil pit (just below the surface organic layer). They were returned to the lab, weighed, dried at 110 C for 24 hours, reweighed and the volume of water driven off calculated as a percent of the volume of the sample.

Since it was desirable to determine what attributes of fencerows rendered them suitable as habitat or as avenues for dispersal, vegetation was sampled in the fall of 1980 in order to correlate the cover of fencerow species with the frequency of chipmunk use, as evidenced by the frequency of capture in live traps. The fencerows in the vicinity of wood 3 were divided into 20 m segments, with each segment centered on a trap location. Since the

traps themselves were 20 m apart, the entire fencerow was inventoried. Certain areas were excluded from consideration due to the activities of the landowners in spraying or burning the brush (fencerows 4 and 9, Fig. 1). In all, 2520 m or 126 20 m segments were analyzed.

Vegetation in the fencerows was divided into three layers: the herb layer (0-1 m), shrub layer (1-3 m) and the tree layer (3 m+). In each layer the cover of each species was recorded using a Braun-Blanquet Index (Mueller-Dombois and Ellenberg 1974). This semiquantitative index records percent cover of each species as falling into one of seven classes (Table 3).

Since the 20 m intervals of fencerow were unmanageable, they were broken down into 2 m subintervals in the case of the herb layer and 5 m subintervals for the shrub and tree layers. Cover index values for each species were recorded in the field, following examination of each subinterval. In addition, various environmental features thought to be relevant to chipmunks were recorded. Cover of rocks and rails was also recorded by Braun-Blanquet index. The term "rails" was broadened to include fallen trees and large branches as well as the remnants of old rail fences. Also two "open" categories were included, one for no herb cover, the other for no shrub cover.

The width of the fencerow was recorded at each 2 m

Table 3.

Braun-Blanquet index used to quantify percent cover in fencerows.

P-P ³ Index	% cover	Functional definition
1	0-0.5	solitary, cover insignificant
2	0.5-1.5	few, cover insignificant
3	1.5-5	numerous, <1/20 cover
4	5-25	1/20-1/4 cover
5	25-50	1/4-1/2 cover
6	50-75	1/2-3/4 cover
7	75-100	3/4-complete cover

subinterval by means of a graduated bamboo pole thrust through the shrubbery from one side to the other. The border of the fencerow for all vegetation strata in the case of very brushy segments was defined by the presence of dense branches in the shrub layer. In the absence of dense shrubbery, the extent of jumbled rocks piled along the fencerow was considered to define the boundary. While cover of trees was recorded between these defined boundaries, tree crowns commonly extended over the field to either side of the fencerow. These were not included in the recorded cover index.

Recorded cover index values for each species and environmental feature in each subinterval were then grouped to obtain a value for each interval. This was done by taking the arithmetic mean of the cover index values in the subintervals. This technique considerably accents the importance of species which had little cover in the subintervals. The class midpoints of the percent cover classes are far from being an arithmetic series, while the index values which replace them were used as though they were. This was necessary to ensure that species of little cover which may be important to chipmunks in some way, or which may be indicative of some environmental condition are not "swamped" or lost from consideration through averaging with species of much greater cover.

Pearson's product moment correlation coefficients were calculated for all possible pairs of variables, these being chipmunk, Peromyscus and Microtus numbers, cover of each plant species and environmental attributes. In addition, the nonparametric Spearman's and Kendall's rank-order correlation coefficients were calculated between chipmunk numbers and all other variables. A multiple correlation coefficient was calculated between chipmunk numbers and a group of variables which the simple correlation coefficients had shown were most strongly correlated to them. A stepwise inclusion technique was employed (Stopher and Meyburg 1979) whereby variables were added to the multiple correlation model in an order selected by an algorithm designed to maximize the multiple correlation coefficient with a small subset of the total number of variables. Since the multiple correlation coefficient is influenced by the number of variables added to the multiple correlation model, regardless of the explanatory power of those variables, an adjusted multiple correlation coefficient was also calculated (Norusis 1978). Additional explanation of this technique is provided in the results section.

All statistical analysis was done using algorithms provided by SPSS software packages (Nie et al. 1970).

RESULTS

In the 1979 trapping season 143 chipmunks were captured an average of 4.6 times each and in 1980 134 animals were captured an average of 5 times each. Mortality over the entire study, almost entirely due to hypothermia during cold nights, totalled 17 fatalities in 1328 captures of 277 individuals.

Chipmunk populations

In the spring of both field seasons, the substantial populations observed in woods 1 and 3 were soon augmented by large numbers of juveniles. These individuals of the spring litter dispersed from their natal burrow soon after weaning. The interval between appearance at the burrow entrance and independence has been variously reported as approximately three days (Yahner 1978a) or one to two weeks (Elliott 1978). The young born in the spring litter grow rapidly and by midsummer are indistinguishable in size and weight from adults once they exceed the weight of 75 g (Smith and Smith 1972). This cut-off point seemed reasonable in this study since only two chipmunks known to be adults were recorded at a weight of 75 grams. This resulted in animals being called "uncertain age individuals" (Table 4). This category made up a varying proportion of the total, largely depending on the timing

Table 4.

Chipmunk population structure in woodlots and fencerows.

Area	Year	Adult Males		Adult Females		Uncertain Age**		Young of Year+		Comments**
		Total	Breeding Summer*	Total	Breeding Spring Summer	MM	FF	MM	FF	
Wood 1	1979	8	8	5	6	2	14	10	4	7
"	1980	7	7	4	4	2				removed
"	1980						1	1	1	immigrants
Fencerow by wood 1	1980			1			1	1	1	1
Wood 2	1979			2	2		2		3	
"	1980	1	1							removed
"	1980									immigrants
Fencerow by wood 2	1980						1	2	1	1
Wood 3	1979	4	4	9	6	4	5	7	14	22
Wood 3	1980	5	5	10	7	5	10	6	10	4
"	"								7	11
										spring-born young only
										summer-born young only

Table 4 continued.

Area	Year	Adult Males		Adult Females		Uncertain Age**		Young of Year†		Comments††
		Total	Breeding Summer*	Total	Breeding Spring Summer	MM	FF	MM	FF	
Fencerows by wood 3	1979	1	1			3	2	1	2	not also caught in woods 2020 m of fencerow trapped
Wood 3 and fencerows	1979	2	1					5	1	moved between woodlot and fencerows
Woods 3, 4 and 5	1979					1		1		moved between woodlots
Fencerows by wood 3	1980	2	1	5	5	1	1	9	8	not also caught in woods 3080 m of fencerow trapped
Wood 3 and fencerows	1980	1	1					6	1	moved between woodlot and fencerows
Woods 3, 4 and 5	1980						1	2		spring-born young only summer-born young only

Table 4 continued.

Area	Year	Adult Males		Adult Females Total	Breeding Spring Summer	Uncertain Age**		Young of Year+		Comments**
		Total	Breeding Summer*			MM	FF	MM	FF	
Wood 4	1979					1		1	1	immigrants
Wood 4	1980	1	1	2	2	2			1	
Wood 5	1979					1	1			immigrants

* no information was collected on which males were in breeding condition during the spring breeding season. In the case of females, lactation demonstrated previous breeding activity.

** animals caught first at weight greater than 75 g; includes large young of year and some overwintered animals not showing signs of reproductive activity.

+ refers to young born in spring only unless otherwise specified

** applies to all of the individuals in the line containing the comment

of the first trapping period following emergence of juveniles from their natal burrows. I found no positive evidence of an animal breeding in the year of its birth, although reports of this exist (Allen 1938, Burt 1940, Pidduck and Falls 1973, Smith and Smith 1972, Yerger 1955).

The chipmunks in this area bred a second time in both 1979 and 1980 (Table 4). This midsummer breeding season has been noted by a number of workers but apparently is a sporadic occurrence in Ontario (Smith and Smith 1972, Pidduck and Falls 1973).

A great deal of variation existed in the numbers of animals breeding in each of the woodlots (Table 4). Wood 1 had a substantial breeding population, with 9.6 individuals per ha in 1979, following weaning of the young in the spring. Numbers of breeding animals were somewhat fewer although entirely comparable in 1980. These breeders were removed from the woodlot.

The breeding population in wood 2 was in marked contrast to this since it consisted of only two females, both of which gave birth in the spring of 1979. The adult male was not trapped and presumably was transient. In the spring of 1980, when the population was removed only one individual, a reproductively active male (509/510) which had not been marked in 1979 was found and transported elsewhere. This individual may have been a midsummer born

offspring of one of the females trapped in 1979 or it may have entered the woodlot after wintering elsewhere.

Wood 3 had a sizeable population of similar density to that of wood 1. In 1979 there were 6.8 animals per ha and in 1980, 7.1 animals per ha, after weaning of the spring litter. Table 4 suggests that not all the females which bred in the spring of 1979 have been accounted for. The six breeding females observed in wood 3 in 1979 would have had to produce six to eight offspring each, depending on whether or not most of the uncertain age individuals had overwintered. A litter size of six is conceivable, but as an average it is probably too high. Although individual litter sizes may run from one to nine individuals, observed population averages for Ontario are 4.9, 5.3 and 2.8 (Pidduck and Falls 1973) and 4.8 to 4.9 (Smith and Smith 1972). Other reported mean litter sizes for various areas in the USA are entirely within this range (Condrin 1936, Yerger 1955, Seidel 1960) and also suggest that the inferred litter sizes here are too large. Litter sizes in 1980 would have been in the neighborhood of 4.3 young per female, which is reasonable.

Litter sizes in wood 1 (1979) and wood 5 (1980) were approximately 5.8 and 3.8 respectively. The midsummer litters produced in wood 3 in 1980 averaged 3.6 weaned offspring. These young were trapped soon after emergence so they probably were aged accurately, but the single

4-day trapping period probably resulted in less than 100% capture of this cohort.

Movements

In 1979, trapping in the series of fencerows around wood 3 (fencerows 1-9, Fig. 1) produced a picture of considerable movement between woodlot and fencerows (Table 4). This movement was not unidirectional. Four of the seven animals (four males, including two adult males, and one female) moved from wood 3 to closely adjacent fencerows 1, 3 and 4 (Fig. 1) and stayed there. The remaining three animals moved back and forth between woodlot and fencerows. One of these (377/378) moved repeatedly between wood 3 and an adjacent fencerow (no. 4) indicating that its home range included 140 m of the fencerow as well as a small area of the wood (radius approx. 20 m) near where the fencerow abutted. Nine captures of this individual showed four crossings of the boundary between woodlot and fencerow. The boundary perhaps appeared more real for the human observer than it did for the chipmunk.

The remaining two movers between woodlot and fencerow moved much farther along the fencerows and did not necessarily originate from a natal burrow in the woodlot. Both of these animals were originally captured near the north end of fencerow 6 in early July. Chipmunk 133/134,

a spring litter male, was later captured in wood 3 near where fencerow 4 abuts it. Probably, it had followed fencerows 2 and 3 to that point. Subsequently it remained in that area and was once caught in the adjacent fencerow 4, 20 m from the woodlot edge. Probably, based on the locations of six captures, it established a home range largely overlapping that of 377/378, encompassing the end of fencerow 4 and the woodlot edge.

Chipmunk 379/380, also a 1979 spring litter male was caught several times around the junction of fencerows 6 and 8. Later it was found in the center of the northern edge of woodlot 3. Rather than having entered wood 3 from the western side where the fencerow came closest to the woodlot, its position would indicate that likely it had moved across the 65 m of open meadow between fencerow 1 and the northern edge of the woodlot. Subsequently it returned approximately 500 m to a point in fencerow 6 very near where it had been captured originally.

Of the animals caught entirely in fencerows in 1979, three (including 1 adult male in breeding condition), were found only in fencerows 3 and 4 and had probably left wood 3. The other six travelled between fencerows 1, 2, 5, 6 and 7 and could not be positively traced to any source which contained breeding females. Of these, 639/670 and 385/386 travelled the furthest, or 300 and 260 m respectively. The rest were observed to travel less than 100 m, perhaps due to few recaptures each. In particular,

uncertain age female 437/438 was found only at the furthest west end of fencerow 2 and one may infer that it moved at least 625 m from the nearest corner of wood 3 or 730 m from the nearest point in the fencerows known to contain a breeding female. This point was in fencerow 10 and the presence of a natal burrow was not detected until 1980. Since this fencerow was not trapped in 1979 it may be regarded as the closest spot which may have contained a burrow.

In 1980, trapping was extended into fencerows 10, 11 and 12, as well as fencerows 13, 14 and 15 around woods 1 and 2, an additional 2380 m. Trapping in fencerows 10, 11 and 12 showed the presence of five lactating females and their progeny. One of these females (135/136) found in fencerow 10 had been marked in fencerow 6 in 1979, 100 m away from her first 1980 capture. Another adult female died in the trap. The fifteen spring-born individuals which were trapped first in fencerows 10, 11 and 12 might easily have been produced by the remaining four females.

Of the fencerow-born chipmunks 687/688 was the most wide-ranging, covering 1300 m between most widely separated points of capture. These were in fencerows 12 and 7, the distance being measured along fencerows. This individual then returned and was caught 480 m back along his route, in fencerow 10. The next most well-travelled chipmunk covered only 200 m between most widely separated

points of capture.

Most of the young chipmunks which crossed woodlot boundaries apparently originated in wood 3 since they were caught either there or in fencerow 4 first. Four of these youngsters adopted the habit of two of the chipmunks caught in 1979; they had home ranges extending from fencerow 4 into adjacent parts of wood 3.

Chipmunk 645/646, a female of the spring litter, travelled from the vicinity of the junction of fencerows 2 and 6 to wood 3 and back to the westernmost end of fencerow 2. This distance is 580 m from its most widely separated points and the animal covered most of it twice. Her locality of birth cannot be determined.

Chipmunk 767/768 followed a similar route for a shorter distance. This individual was caught first in fencerow 3 so may well have originated in wood 3, was caught again in the nearby edge of wood 3 and later at the junction between fencerows 6 and 2. Chipmunk 673/674 was caught near the junction of fencerows 6 and 2 and later at various points closer to wood 3 and finally inside the northwest edge.

Chipmunk 589/590, also originally tagged in 1979, was a reproductively active male when caught in 1980 and as such was somewhat anomalous in leaving wood 3 for the nearby fencerow. He was caught first in wood 3 and later in fencerow 3 immediately to the west. Subsequently he

was caught both in this nearby fencerow and also in the edge of the woodlot. Probably his home range spanned both part of the woodlot and the nearby fencerow.

Of those chipmunks caught in fencerows 1 to 9 in 1980, only two out of 14 could be assigned an origin in fencerows 10-12 from their locations of first capture. Several were caught a number of times in fencerows close to wood 3 as well as in the wood so could safely be attributed to some female in the wood. The majority of chipmunks in fencerows 1-9, then, were likely born in wood 3 and moved out into the fencerows. Probably some of the movements across woodlot boundaries observed on the part of chipmunks caught first in fencerows 1-9 were movements back through areas which the chipmunks had experienced previously but this can not be confirmed.

A marked difference was seen in the behavior of the chipmunks in the sections of fencerow trapped only in 1980 (fencerows 10, 11 and 12). These sections contained the only breeding females found anywhere in this group of fencerows. Also none of the chipmunks captured in these sections was ever observed to enter wood 3.

The fencerows adjacent to woods 1 and 2 presented a somewhat different picture of chipmunk movements. The important difference here was that the population in the woodlots from which animals might have moved into the fencerows had been removed. Interestingly, animals left

wood 1 in 1980 even though there were not many animals there. Two animals entered the wood from points unknown and stayed. Another young animal, after being caught in the wood in July left for fencerow 13 to the west. No chipmunks were ever caught in fencerow 14 east of wood 1. The fencerow west of wood 1 was long and very wide. Apparently, some breeding occurred since one female which had been lactating earlier in the spring died in a trap there. At the time of capture its vulva was swollen indicating estrus although mating could not be presumed due to the absence of adult males. There were other fencerows nearby which conceivably could have held males. Also fencerow 13, although it became very sparse to the west of the region trapped (660 m from wood 1), may have served as an avenue for movement of chipmunks from the nearest woodlot 1000 m further west. Three young were caught near where the female was trapped and may have been her offspring. Although the three other chipmunks also caught in wood 1 could not be satisfactorily assigned to any point of origin, they may have been from this fencerow as well.

Wood 2 showed a very similar pattern of immigration from fencerows, with some return to the fencerows. It was quite evident that animals were entering wood 2 by moving along fencerow 15 from the east. This fencerow connected to several other fencerows which were never trapped. Five

chipmunks were found in fencerow 15 but none were reproductive. One of these entered wood 2 and one first caught in wood 2 entered the fencerow. Interestingly one of the chipmunks caught first in wood 2 (633/634) embarked on one of the longest movements recorded in this study. Between 21 and 25 June this animal moved 1300 m from the center of wood 2 to fencerow 13, 160 m to the west of wood 1. This distance is quite comparable to that covered by 687/688, mentioned previously, which moved along the fencerows to the north of wood 3. Parenthetically, it might be noted that 633/634 was not born in wood 2 so the figure given for the distance it travelled does not take into account any distance covered to get there.

The trapping that was carried out in woods 4 and 5 in 1979 revealed a picture of chipmunk populations which was very similar to that found in woods 1 and 2 following removal trapping. Populations in 1979 appeared to be due to the influx of animals from breeding sites elsewhere since no reproductive animals were present. The inter-woodlot movements of chipmunks which were observed supported this. One male (349/350) moved from wood 3 to wood 5 sometime between 28 June and 18 July. The distance between captures in wood 3 and wood 5 was 1470 to 1560 m depending on the route taken along the fencerows. This is assuming that the animal did follow fences rather than moving across open fields. The straight line distance

between successive points of capture would have been 1140 m, but there is no evidence that chipmunks travel in straight lines. Some cover may have been afforded by crops of corn, oats or alfalfa along the route but evidence of chipmunks using this type of habitat is completely lacking. None of the fences in this region was sufficiently well developed to be called fencerows. Some of them had intermittent and widely separated patches of prickly ash but most were just barbed wire. One chipmunk (157/158) moved 430 m between wood 4 and wood 5 between 16 and 18 July 1979. The fencerow between the two woods had only scattered clumps of prickly ash, but in 1979 the field between woods 4 and 5 was planted in oats so plenty of cover would have been available. Again it cannot be determined whether the animal actually followed a fenceline or not except to note that following the fenceline would have been the shortest route between the successive points of capture.

Similar patterns of movements were observed in 1980. Both woods 4 and 5 contained breeding males and females in 1980 and these apparently had their litters successfully. The breeding male in wood 5 was 157/158 mentioned above, which had successfully overwintered. The breeding female in wood 4 had also been caught in 1979 in the same woodlot and had also overwintered. The origins of the other breeders could not be determined but since they had bred

in March and April, they almost certainly had overwintered where they bred.

Two chipmunks born in the spring of 1980 left wood 4 for wood 3 covering 890 and 587 m respectively, 460 m of it through areas completely lacking in woody cover and presumably along the fence leading directly from one of the woods to the other. One midsummer-born female from wood 3 travelled in the opposite direction between 7 and 11 September 1980. Another female (743/744) travelled between wood 4 and wood 5. The overall picture, then, is one of interwoodlot movements occurring sporadically over the summer, although, unlike chipmunks moving through the fencerows, these animals showed no tendency to return from whence they came.

The considerable number of dispersing individuals noted in this study permit analysis of the age structure of this segment of the population. Young males were the most numerous category among the animals dispersing (Table 5). The observed sex ratio of approximately 2:1 (males:females) was remarkably consistent over both years of the study. The hypothesis that the sex ratio was 1:1 can be rejected at the 0.05 level ($\chi^2=5.4$, 1 degree of freedom) if data from both years are combined. Chipmunks observed only in fencerows 10, 11 and 12 and apparently progeny of breeding females in those fencerows were not considered dispersers. The data are insufficient to realistically record the distances over which these

Table 5.

Dispersing chipmunks*

	1979 Numbers	1980 Numbers
Adult males	3	1
Adult females	0	0
Uncertain age males	7	3
Uncertain age females	6	4
Young of year males	9	16
Young of year females	4	7
Total	29	31
Sex Ratio Males:Females	19:10	20:11

* Includes all chipmunks which crossed woodlot boundaries as well as those chipmunks caught in fencerows nos. 1-9 and 15 which had no breeding females.

chipmunks actually moved, precluding the suggestion that one sex tended to move farther than the other. Since females colonized woods 4 and 5 in 1979, they were effective colonists just as the males were.

Woodlot habitat analysis

Assessment of habitat quality presupposes that the factors perceived as important by the animals could be identified and quantified by a human observer. Assuming that important variation in habitat quality from place to place within a woodlot exists, one can compare the distribution of animals over the area with measured environmental attributes which are hypothesized as being important. To quantify the dispersion of chipmunks the number caught at a particular trap location can be considered an index of the amount of chipmunk use of that area. The distribution of chipmunk captures over each woodlot appeared to be non-random. If the chipmunks cued on some aspect of the environment, the patterns of use of particular areas shouldn't change much from year to year. The Pearson product moment correlation coefficient, comparing the numbers of chipmunks caught at each trapping location in wood 3 in 1979 with the numbers caught at the same locations in 1980 was 0.352 (t-test with 247 degrees of freedom, $p=0.001$), a weak correlation but larger than would be expected to occur by chance.

Whatever factors in the habitat cause chipmunks to adopt the dispersion that they do, it appears that either the habitat is not "full" and the chipmunks are choosing among a number of suitable areas or some factors other than quality of habitat such as perhaps social behavior or undetermined stochastic factors are influencing choice of areas occupied.

In the spring of 1980, an effort was made to determine what factors influence the chipmunk's selection of appropriate habitat in which to locate burrows. Data, of course, could only be collected on positions of burrow entrances. The locations of the hibernacula might be up to a maximum of 10 m from the entrance (Yahner 1978a). Since the hibernacula cannot be located it must be assumed that the choice of burrow entrance location is the initial choice made in locating the hibernaculum and is governed by a related set of criteria.

In wood 1 I located 28 burrow entrances by observing tracks on the snow or animals once the snow had disappeared. Data were collected at burrow entrances on 22 April when there were many small temporary puddles throughout the woodlot. Since puddles were numerous in the spring, it was thought that this might be a critical time of year with respect to chipmunk survival and hence some of the factors governing choice of location might be particularly evident. The soil appeared to be saturated

Table 6.

Habitat analysis in wood 1 comparing conditions at burrow entrances to randomly located points. Data collected on 22 April 1980.

a. Pairwise comparisons

	Burrow entrances	Random points	Test of significance
Mean soil moisture (% by volume)	42.1	42.7	Student's t-test $t = -0.374$ with 54 degrees of freedom $p = 0.709$
Mean depth to frost (cm)	34.0	37.4	Mann-Whitney U-test $p = 0.413$
Mean distance to nearest standing water (m)	6.5	3.7	Mann-Whitney U-test $p = 0.004$

b. Contingency table analysis of numbers of burrows or random points falling on mounds, intermediate areas or depressions.

Local topography	Burrow entrances	Random points	Test of significance
Mounds	22	14	Contingency chi-square=6.611 with 2 degrees of freedom $p = 0.037$
Intermediate areas	5	7	
Depressions	1	7	
Total	<u>28</u>	<u>28</u>	

and at eleven of the locations sampled (seven at randomly located points, four at burrow entrances) water ran into the soil pits. This happened at a saturation of roughly 40% (by volume) or greater, clearly indicating danger of burrow flooding.

Soil moisture measurements made at the chipmunk burrows and random points were nonsignificantly different (Table 6) indicating that chipmunks are not or cannot select burrow locations in areas which are drier than those typical of the woodlot as a whole. The lack of selection for dry areas was likely because the ground was quite uniformly moist and dry areas were not to be found. A comparison of depth to frost line at burrow entrances and random points shows that chipmunks were not selecting areas which thawed faster (Table 6). A non-parametric test was employed here since the assumption of homogeneity of variances required for the use of parametric statistics could not be supported. Locations at which the soil was completely thawed (six burrow entrances and five random points) were not included in this analysis. Mean distances to the nearest standing water measured from burrow entrances and random points indicate that chipmunks were significantly further from standing water than would be expected under a hypotheses that they were not selecting the spot with some criterion in mind. However, the difference between the two means is not great and it

is doubtful whether this would have made any difference with respect to soil moisture in the vicinity of the hibernaculum. The maximum that any chipmunk could manage was 20.2 m between his burrow entrance and standing water.

Chipmunk burrows and random points were classified as to their position with respect to surrounding terrain, namely whether they existed on a mound, depression or intermediate area between the two. The data were analyzed by means of a chi-square contingency table, the null hypothesis being that the topography would vary independently of whether the point was randomly located or at a burrow entrance. The figures indicate that chipmunks prefer to have their burrow entrances on mounds.

Fencerow habitat analysis

Fig. 2 shows the results of a multiple correlation between the numbers of chipmunks caught at each fencerow trap location and a series of variables characterizing the cover of various species of vegetation and various environmental attributes. The number of independent variables which could be included in a given computer run (15) was set by the capacity of the computer, a Xerox CP-V, to store and handle matrices of large size. The 15 variables most strongly correlated to chipmunk numbers (Table 7) were used. Note that not all were significantly correlated.

Figure 2.

Change in the multiple correlation coefficient,
R., and adjusted multiple R. with addition of new
variables by means of stepwise inclusion.

Table 7.

Simple correlation coefficients between numbers of chipmunks captured in fencerow traps and vegetation cover and other selected attributes of fencerows surrounding wood 3.

Correlations are computed as parametric Pearson product moment correlation coefficients and nonparametric Spearman's and Kendall's rank order correlation coefficients.

ns $p > 0.05$ * $p < 0.05$ ** $p < 0.01$

Cover species	Pearson's r	Signif.	Spearman's rho	Signif.	Kendall's tau	Signif.
Open herb layer	0.0073	ns	-0.0218	ns	-0.0144	ns
Open shrub layer	0.0296	ns	0.0281	ns	0.0153	ns
Rocks	0.3193	**	0.3605	**	0.2740	**
Rails	0.3126	**	0.3510	**	0.2677	**
Width	0.2390	**	0.1227	ns	0.0945	ns
<u>Peromyscus</u>	-0.0194	ns	0.0665	ns	0.519	ns
<u>Microtus</u>	-0.0095	ns	-0.1303	ns	-0.1171	ns

Table 7 continued.

Cover species	Pearson's r	Signif.	Spearman's rho	Signif.	Kendall's tau	Signif.
<u>Acer negundo</u>	0.2062	*	0.1690	ns	0.1369	ns
<u>Crataegus</u>	0.3582	**	0.3042	**	0.2631	**
<u>Fraxinus americana</u>	-0.1389	ns	-0.1331	ns	-0.1081	ns
<u>Fraxinus nigra</u>	-0.1545	ns	-0.1621	ns	-0.1409	ns
<u>Quercus macrocarpa</u>	0.1035	ns	0.0624	ns	0.0551	ns
<u>Tilia americana</u>	0.2201	*	0.0624	**	0.2322	**
<u>Ulmus americana</u>	0.0395	ns	0.0050	ns	0.0051	ns
<u>Parthenocissus</u>	-0.0303	ns	-0.1341	ns	-0.1098	ns
<u>Viburnum lentago</u>	0.2651	**	0.1319	ns	0.1135	ns
<u>Vitis riparia</u>	0.0454	ns	0.0373	ns	0.0328	ns
<u>Zanthoxylum americanum</u>	-0.0937	ns	-0.1319	ns	-0.1057	ns
<u>Arctium</u>	0.01785	*	0.2025	*	0.1688	*

Table 7 continued.

Cover species	Pearson's r	Signif.	Spearman's rho	Signif.	Kendall's tau	Signif.
<u>Aster</u>	-0.0848	ns	-0.1287	ns	-0.1074	ns
<u>Bidens</u>	0.1819	*	0.2348	**	0.2014	**
<u>Cirsium</u>	0.0427	ns	0.0048	ns	0.0026	ns
<u>Fragaria</u>	-0.1853	*	-0.2754	**	-0.2240	**
<u>Geum</u>	-0.0458	ns	-0.1481	ns	-0.1174	ns
<u>Grasses</u>	-0.1808	*	-0.2354	**	-0.1830	**
<u>Lithospermum</u>	-0.0885	ns	0.0695	ns	0.0593	ns
<u>Moss</u>	-0.2740	**	-0.2163	*	-0.1878	*
<u>Potentilla</u>	-0.0998	ns	-0.0852	ns	-0.0727	ns
<u>Ribes</u>	0.1362	ns	0.1862	*	0.1625	*
<u>Rubus</u>	0.0701	ns	0.1822	*	0.1555	*
<u>Solidago</u>	-0.0940	ns	-0.0410	ns	-0.0325	ns
<u>Taraxacum</u>	-0.0924	ns	-0.1765	*	-0.1502	*

Table 8.

Results of a multiple correlation between chipmunk numbers trapped in fencerows and selected environmental variables showing change in multiple correlation coefficient with addition of new variables by means of stepwise inclusion.

Order of variable addition	Variable	Multiple R ²	Signif. [†]	Partial R ²	Signif. ^{††}
1	<u>Crataegus</u> sp	0.12833	**	0.12833	**
2	Rails	0.21129	**	0.09517	**
3	<u>Viburnum</u> <u>lentago</u>	0.24688	**	0.04512	*
4	Width	0.26902	**	0.02939	ns
5	<u>Bidens</u> sp	0.28810	**	0.02610	ns
6	<u>Fraxinus</u> <u>americana</u>	0.20500	**	0.02373	ns
7	<u>Ribes</u> sp	0.31700	**	0.01726	ns
8	Rocks	0.32586	**	0.01297	ns
9	<u>Fraxinus</u> <u>nigra</u>	0.33216	**	0.00934	ns
10	Moss	0.33945	**	0.01091	ns
11	Grasses	0.34679	**	0.01111	ns
12	<u>Arctium</u> <u>minus</u>	0.34900	**	0.00338	ns
13	<u>Fragaria</u>	0.34996	**	0.00146	ns
14	<u>Acer</u> <u>negundo</u>	0.35119	**	0.00189	ns
15	<u>Tilia</u> <u>americana</u>	0.35130	**	0.00013	ns

** $p < 0.01$

* $p < 0.05$

ns $p > 0.05$

† tests null hypothesis that multiple $R = 0$ by means of an F test with k and $N - k - 1$ degrees of freedom where k is the number of variables already brought into the multiple correlation and N is the sample size (126)

†† tests null hypothesis that partial $R = 0$ by an F test with 1 and $N - k - 1$ degrees of freedom

Table 2.

Upper triangular matrix showing significance and sign of Pearson's product moment correlation coefficients between all possible pairs of variables quantified for the fencerows surrounding wood 3.

Section a: upper left-hand part of matrix

" b: upper right-hand part of matrix

" c: lower right-hand part of matrix

Legend: ns correlation coefficient not significantly different from zero (t-test with 124

degrees of freedom) $p > 0.05$

+* correlation positive, $p \leq 0.05$

+++ correlation positive, $p \leq 0.01$

-* correlation negative, $p \leq 0.05$

-** correlation negative, $p \leq 0.01$

continued...

Table 9a.

	o <u>Peromyscus</u>											
<u>Peromyscus</u>	o	ns	Open herb layer	o	ns	Grasses	o	ns	Rocks	o	ns	Rails
Open herb layer	o	ns	Grasses	o	ns	Rocks	o	ns	Rails	o	ns	Open shrub layer
Grasses	o	ns	Rocks	o	ns	Rails	o	ns	Open shrub layer	o	ns	Arctium
Rocks	o	ns	Rails	o	ns	Open shrub layer	o	ns	Arctium	o	ns	Aster
Rails	o	ns	Open shrub layer	o	ns	Arctium	o	ns	Aster	o	ns	Bidens
Open shrub layer	o	ns	Arctium	o	ns	Aster	o	ns	Bidens	o	ns	Cirsium
Arctium	o	ns	Aster	o	ns	Bidens	o	ns	Cirsium	o	ns	Fragaria
Aster	o	ns	Bidens	o	ns	Cirsium	o	ns	Fragaria	o	ns	Geum
Bidens	o	ns	Cirsium	o	ns	Fragaria	o	ns	Geum	o	ns	Parthenocissus
Cirsium	o	ns	Fragaria	o	ns	Geum	o	ns	Parthenocissus	o	ns	Ribes
Fragaria	o	ns	Geum	o	ns	Parthenocissus	o	ns	Ribes	o	ns	Lithospermum
Geum	o	ns	Parthenocissus	o	ns	Ribes	o	ns	Lithospermum	o	ns	Microtus
Parthenocissus	o	ns	Ribes	o	ns	Lithospermum	o	ns	Microtus	o	ns	
Ribes	o	ns	Lithospermum	o	ns	Microtus	o	ns		o	ns	
Lithospermum	o	ns	Microtus	o	ns		o	ns		o	ns	
Microtus	o	ns		o	ns		o	ns		o	ns	

Table 9c.

Moss	o	Moss	
Potentilla	o	+++	Potentilla
Rubus	o	ns	-
Solidago	o	ns	ns
Taraxacum	o	ns	+
Vitis	o	ns	ns
Width	o	ns	ns
Acer negundo	o	+++	+++
Crataegus	o	ns	ns
Fraxinus americana	o	ns	ns
Fraxinus nigra	o	ns	ns
Quercus macrocarpa	o	ns	ns
Tilia americana	o	ns	ns
Ulmus americana	o	ns	ns
Viburnum lentago	o	ns	ns
Zanthoxylum americanum	o	ns	ns

Table 12. Correlation matrix showing significance and sign of the Pearson product moment correlation coefficients comparing the "rocky and open" and the "Zanthoxylum" groups of species and environmental attributes from fencerows surrounding wood 3.

Legend as in Table 9.

	Open herb layer	<u>Aster</u>	<u>Fragaria</u>	<u>Geum</u>	<u>Parthenocissus</u>	<u>Moss</u>	<u>Potentilla</u>	<u>Solidago</u>	<u>Taraxacum</u>	<u>Zanthoxylum</u>
Rocks	ns	ns	-**	-**	ns	-**	ns	-**	ns	-**
Rails	-**	-**	-**	-**	-**	-**	ns	-**	-*	-**
Open shrub layer	-**	-**	-**	-**	ns	ns	ns	-**	ns	-**
<u>Arctium</u>	ns	-**	-**	-**	ns	-**	-**	-**	-**	-**
<u>Bidens</u>	ns	ns	-**	-**	-*	-*	ns	-*	ns	ns
<u>Ribes</u>	-**	-**	-**	-*	ns	-**	-*	-*	ns	-*
<u>Litho-spermum</u>	-*	ns	ns	ns	-*	ns	ns	ns	ns	ns
<u>Rubus</u>	ns	ns	-*	ns	-*	-*	ns	ns	ns	ns
<u>Tamias striatus</u>	ns	ns	-*	ns	ns	-**	ns	ns	ns	ns
<u>Tilia americana</u>	ns	+	-*	-*	ns	-*	ns	ns	-*	-**

To sort out that set of independent variables which together show the maximum correlation with the chipmunk numbers trapped, a forward (stepwise) inclusion technique was employed, whereby variables were added one by one with a multiple correlation coefficient R calculated after each addition (Stopher and Meyburg 1979). At each step, the SPSS algorithm automatically selects the next variable to be added after calculating a partial correlation coefficient for each of the variables not in the equation. An F statistic is calculated for each of the partial correlation coefficients (Norusis 1978) and the variable with the largest F value is added in the next step. Table 8 shows the order in which variables were added by means of this procedure and the squared multiple correlation coefficients calculated after their addition.

The squared partial correlation coefficients calculated before the addition of each variable represent the proportional influence which each variable has in explaining variation in the dependent variable, over and above that variation explained by the independent variables already in the equation. The squared partial correlation coefficient, then, which is associated with each variable in Table 8 is calculated before the addition of that variable and is automatically the largest partial correlation among those variables not yet in the equation.

Note that the partial correlation coefficients are

considerably less than the simple correlation coefficients which compare each of the independent variables with the dependent variable. This is due to the high frequency of intercorrelations among the independent variables. Table 9 presents an upper triangular matrix showing the significance level for all the Pearson product moment correlation coefficients comparing each variable with every other variable. For those correlation coefficients which are significant, the sign (positive or negative) is also shown. Since the correlation coefficients are uniformly weak, the sign suffices to show the nature of the association between any two variables.

The high frequency of intercorrelations ensures that the simple correlations between a series of variables and the dependent variable are nowhere near being additive. In fact, the partial correlation coefficients demonstrate that after the first three variables have been added to the equation by the stepwise inclusion procedure, the addition of further variables does not increase the multiple correlation coefficient further by any significant amount.

Due to the nature of the least squares technique, the addition of new variables to the equation, even though some of those variables may not themselves be significantly correlated to the dependent variable will cause the multiple correlation coefficient to increase by

a small amount, with the addition of each new variable. This is due to the inclusion of chance variations in the variables being incorporated in the calculations of multiple R (Thorndike 1978). To remove the effect of sample size, an adjusted R was calculated (Norusis 1978) which is not sensitive to the number of variables included. It can be seen that the difference between unadjusted and adjusted R squared values becomes greater with the addition of more variables (Fig. 2), as is expected.

One cautionary note must be added with respect to the interpretation of the variables and their importance in contributing to the magnitude of multiple R . The order given here was chosen by the SPSS algorithm for stepwise inclusion into a multiple correlation model. There are other methods of selecting a subset from a group of variables which also seek to explain a maximal amount of the variation in the dependent variable (Lindeman, et al. 1980). The use of one of these alternative methods might easily have resulted in a somewhat different sequence of variables than was obtained by stepwise inclusion. The important point to note is that a very few variables do suffice to bring the value of multiple R to the highest level which it is able to attain and the addition of more variables subsequent to that does not increase R more than randomly generated data could.

Simple correlation coefficients (Table 9) between the various factors quantified indicated that two groups of associated variables existed and that the members of each group were positively correlated to members of the same group and negatively correlated to members of the other group when such correlations were statistically significant (Tables 10, 11 and 12). Species commonly associated with prickly ash will be referred to as the "Zanthoxylum" group, since this thorny shrub seemed to be ecologically dominant. Members of the other, called the "rocky and open" group, typically had an open shrub layer and were commonly associated with rocks.

Some of the correlations presented in this scheme are highly predictable artifacts of the sampling technique. For example, rocks, rails and open shrub layer are negatively correlated with prickly ash cover because the Braun-Blanquet cover index presents proportions of an area covered. Naturally a high proportion of openness in the shrub layer is associated with a lower proportion of not open, here commonly due to the presence of prickly ash. When a lot of the fencerow area was covered by rocks and rails (including deadfall), less of the total was covered by Zanthoxylum. In spite of these considerations there are two natural groupings of plant species, within each of which the members tend to be positively associated.

Since the trees of the fencerows do not provide a

great deal of shade to the understory, most trees do not fit into either of these groups. An exception is basswood, which shows a positive correlation to some of the species in the "rocky and open" group, but not because of an artifact of sampling since trees were not in the same stratum as the shrubs and herbs. Apparently basswood thrives in an environment not occupied by Zanthoxylum and its associates. A single positive correlation is noted between basswood and Aster spp., part of the "Zanthoxylum" group. The reason for this is not clear. This could be a spurious correlation, a possibility, perhaps expected considering the number of simple correlations which have been computed. On the other hand, not all the species in either group are adapted to an entirely similar suite of conditions and a single species with a somewhat different range of environmental tolerances is not surprising. As Table 10 shows, chipmunks fit into this pattern well, as part of the "rocky and open" group.

DISCUSSION

Recolonization ability

I have shown that chipmunk movement from a woodlot to reestablish a population in unoccupied habitat elsewhere is relatively common, and that it is likely that some individuals will arrive at any unoccupied site over the course of a summer. The immigrating individuals may not succeed in establishing a breeding population since considerable overwinter mortality is a normal and not easily predictable aspect of chipmunk life (Tryon and Snyder 1973). Furthermore the inexperience of the animals in a new location would make establishment and breeding a chancy process. Nevertheless, recolonization can be successful as shown by the animals which immigrated to woods 4 and 5, overwintered, and bred there in 1980.

Several reports in the literature document movements of chipmunks. Almost all deal with movements through continuous forest since it is commonly accepted that the chipmunk is a forest animal and should be studied there. However, Banfield (1974) asserts that chipmunks inhabit fencerows and stonepiles with sufficient cover. Dunford (1970) studied chipmunk behavior in a fencerow but the fencerow in his study was similar to a hardwood forest, being 5 to 6 m wide and composed of black cherry and shagbark hickory with dense undergrowth and a thicket of

aspens on one side. The only previous study to document movement of chipmunks between woods and fencerows (Wegner 1976) showed that such movements were relatively common, although his traplines extended only 100 m at most into the fencerows from the woodlot boundary. Thus there is no realistic picture of distances travelled through fencerows in the literature, nor is there any reasonable picture of the nature of fencerow populations.

My results indicate that the distances over which chipmunks can travel are not limited by an absence of brushy cover in the fencerows. The lack of habitat of sufficient quality to allow chipmunks to reside for some time while moving may restrict the number of animals which enter and move along particular routes or corridors. Many more animals, after all, were noted moving through the fencerows around wood 3 than moved along the fenceline south of wood 3. Thus presence of brushy fencerows may facilitate dispersal, although it is not an absolute requirement. No animals were found to cross the South-Castor River, even though this creek is only 4 m wide in midsummer.

Young males are much more likely to move considerable distances than are females (Table 5). Various other workers have also observed that males are more likely to disperse. Burt (1940) observed that most movements of home range were made by young animals and adult males.

Seven of eight animals which he observed to move were males and the eighth was a young female which moved the shortest distance of all. Yerger (1953) found a similar dearth of home range movements among adult females, although he only observed six animals which moved out of 40 marked, a sample too small to realistically establish proportions. All movers were males, three young and three adults. The distances of movement recorded in Burt's study were 205 to 640 m and those mentioned in Yerger's study were 95 m to 228 m. In addition, Yahner (1978a) recorded mean distances of shifts in home range in a 5 ha woodlot in Ohio. Distances of shifts to new home ranges averaged 54.1 m for males (maximum 125 m) and 27.8 m for females (maximum 55.5 m). No doubt the maximal distances noted were limited by the perimeter of the woodlot.

It is worthwhile to consider the nature of the habitat through which movements can occur, since the longer movements through more open areas allowed chipmunks to enter new and occasionally empty habitat. Three chipmunks were found to move between woods 3 and 4 in the summer of 1980 (Table 4). These animals probably travelled the fenceline which led almost directly from the southeast corner of wood 3 to the northwest corner of wood 4 as a corridor. If this fenceline was not followed, movement must have been through a hay meadow (on one side of the fence) or an alfalfa field and a cornfield (on the

other side of the fence). How the chipmunks could navigate through such trackless habitat is not known. There is no evidence of chipmunks' navigational ability over long distances. Layne (1957) showed that homing ability, or ability of an animal to return to its home range once released some distance away, was restricted to fairly short distances. Only one of his transported animals was able to return over a distance more than 236 m. This individual returned after being released 365 m from its burrow.

The chipmunks trapped in the fencerows in this study apparently followed fencerows when moving between successive points of capture. A few movements took place, however, across the 65 m of meadow between the northwest corner of wood 3 and the nearest fencerow (no. 1). This is consistent with the observation of Wegner (1976) that chipmunks rarely enter fields. Forsyth and Smith (1973) observed one chipmunk which regularly travelled across 70 m of open field. Oxley et al. (1974) found that chipmunks were reluctant to cross roadways having more than 20 m between adjacent forest margins.

In order to travel between wood 3 and wood 4 an animal would have to travel over extensive areas of grass, even if it were following the fenceline. There were isolated small clumps of prickly ash along this fenceline, but the animals would have had to negotiate virtually the

entire distance without woody cover. An animal moved from wood 3 to wood 5 in 1979. It is not known what route it took, but it may have been by way of wood 4 and along the same stretch of barbed wire fence. In addition, chipmunk 633/634 left wood 2 and travelled to the fencerows west of wood 1 in 1980. There were no fencerows leading along this route so he must have followed the grassy verges of the gravel road. This would have taken this individual on a very direct route between the successive points of capture, from alongside wood 2 to alongside wood 1. This distance, also, was covered in a maximum of four days.

One might consider, as well, the type of environment which the chipmunks left, when they began moving. Juvenile chipmunks are subordinate to adults and although they can acquire and defend a home range 15-18 days after emergence from the natal burrow (Elliott 1978), they are excluded from home ranges of adults (Ickes 1974, Mares et al. 1976). The home range of a chipmunk is a loosely defined area with a central defended area of about 12 m in diameter surrounding the burrow system (Elliott 1978). The remainder of the home range overlaps broadly with the home ranges of neighbors (Dunford 1970, Forsyth and Smith 1973). Yahner (1978a) found that the core areas of young animals were quite unstable compared to those of adults with shifts being made every six weeks on the average rather than every four months. Apparently, the individual

spacing behavior regulates population density (Ickes 1974, Mares et al. 1976) with the subordinate animals being forced to leave if unable to locate an unoccupied burrow system (Tryon and Snyder 1973). Although the population densities observed in woods 1 and 3 were not as high as some densities reported in the literature, this does not necessarily mean that the woodlots had a large number of adequate sites left vacant.

An obvious explanation for the departure of young individuals is that they were leaving more densely populated areas for areas with a lower density of adults and hence a lower frequency of agonistic interactions. The interchange noted between wood 3 and adjacent fencerows was not unidirectional toward the fencerows, however. Over both years, among the 16 chipmunks which were caught in both wood 3 and fencerows, 7 or 43.7% were last caught in the woodlot. Social pressure, then, was not sufficient to prevent animals from returning to the woodlot.

Evidence may be gathered elsewhere. Those woodlots which had a very low density of chipmunks and thus too few resident adults to apply a motive force to juveniles also supplied emigrants to their surroundings. Chipmunks left woods 1, 2, 4 and 5 in years when few or no adults were present. Obviously social pressure is not a requisite for the initiation of movement away from a woodlot. The true

cause of these movements is not clear at present.

Chipmunk habitat

The densities of animals recorded in my woodlots fall well below the maximum reported by other workers. Yerger (1953) summarized the literature available and found densities from 1.0 per hectare to 23.9 per hectare from seven other studies as well as his own. Three of the seven studies produced density estimates less than my highest figure of 9.6 per ha for wood 1 in 1979. The densities calculated for woodlots 1 and 3 in this study, then, should be regarded as moderate. There have been no analogous determinations of density for the province of Ontario, so it is not possible to compare these results with others derived from a similar latitude. Most workers do not present chipmunk densities since they are difficult to calculate given capture data from a grid in continuous habitat. All the chipmunks with home ranges spanning the grid edges cannot be included easily since doing so would artificially inflate the estimate. This is not a problem in small woodlots.

My data indicate that it would be inappropriate to develop any deterministic model for the dispersion of chipmunks over either woodlots or fencerows. The weak correlation between the numbers of chipmunks present at a particular trapping location in wood 3 between 1979 and

1980 demonstrates this. The correlation was highly significant, however, so one must suspect that certain factors of the habitat are involved in influencing the animal's choice of location. There are various reasons why the correlation would be weak in addition to the effects of the habitat on the dispersion of the animals. The chipmunks commonly became very trap-happy, although some more so than others. This might have increased the number of captures in the vicinity of the burrow of a trap-happy animal. Social behavior of the animals may have been involved in restricting subordinate individuals from occupying more desirable areas in which a few resident adults had home ranges (Dunford 1970, Ickes 1974, Mares et al. 1976, Yahner 1978a, 1978b, 1978c, Yerger 1953). There is no indication that all the favorable areas were occupied in either 1979 or 1980. If different favorable areas were occupied in different years, the correlation between years would have been weakened.

The measurements of conditions surrounding burrow entrances made in the spring of 1980 was an attempt to elucidate some of the factors governing the chipmunk's choice of particular areas as suitable for burrow locations. It was suspected that the presence of sites suitable for burrows might be a requisite for the survival of chipmunks in an area. Several studies have documented the dispersion of chipmunk activity over the home range

and are in general agreement that both foraging activity and agonistic behavior are most concentrated in the vicinity of the burrow entrance (Elliott 1978, Ickes 1974, Yehner 1978c). The characteristics of this central area, then, would be critical for the welfare of the animal.

One must interpret the results with caution since the tendency to locate burrows on mounds would perhaps result in the burrows being further away from water which lies in the lower of the depressions. The proximal factors influencing chipmunks to locate their burrows on mounds are not entirely clear, then. They may have a preference for mounds and the greater lookout these provide or a dislike of having water run down the burrows in a heavy rainstorm. It is not evident that the burrows were in ground that was any drier than was typical of the woodlot generally, but the reason may be, to reiterate, that such spots simply were not to be found.

The pattern of dispersion of chipmunks over fencerows was weakly correlated from year to year in a fashion similar to that of wood 3. However, the chipmunks in the fencerows were mainly immature and perhaps the spacing behavior of resident adults would have been of lesser importance in influencing dispersion. The same stochastic factors operating in the woodlots would be operating in the fencerows, with the additional problem that more of the individuals were inexperienced.

Considering the poor correlation between years, the maximum multiple correlation coefficient of approximately 0.50 that was obtained between chipmunk numbers trapped in the fencerows and the characteristics of the habitat surrounding the trap locations is perhaps the maximum that might be anticipated. This exercise establishes the lack of a close correspondence between those factors of the environment measured and the preferences of the chipmunks.

The simple correlation coefficients might be of equal value in illuminating which factors out of all those quantified are important. Although some of the correlations between chipmunks and aspects of the habitat (Table 7) may be spurious since with all statistical tests there is a finite but small chance of producing an erroneous result, no doubt the majority are truly indicative of a relationship. Establishing the causal basis for any such relationship is difficult. Chipmunks might cue in on various aspects of the environment such as soil moisture or soil texture in a fashion similar to some plants. The inference of causality in any relationship between animals and the environment derived from correlations between factors which are themselves intercorrelated in multifarious ways (Table 9) is predictably difficult (Blalock 1964).

The positive correlation between chipmunks and members of the "rocky and open" group (Table 10) and

negative correlation with members of the "Zanthoxylum" group (Table 12) is important with respect to one's conclusions regarding the suitability of these fencerows as corridors allowing chipmunk dispersal across a landscape. The presence of prickly ash as a major component of the vegetation here might otherwise be considered a feature rendering the fencerows in this particular study area different and perhaps much more favorable for chipmunk habitation and travel than the fencerows commonly seen in much of agricultural southern Ontario. It does provide considerable cover near the ground and prevents trampling by cattle ranging in the adjacent fields. This analysis, on the other hand, indicates that Zanthoxylum is not a positive factor so far as chipmunks are concerned and may actually have a negative influence on fencerow habitat suitability. It is impossible, at this level of analysis, to say which particular aspects of the environment were directly perceived by the chipmunks in either a positive or a negative sense. It does seem evident that the "Zanthoxylum" group as a whole did not provide a favorable or preferred environment.

There is no reason to believe that a chipmunk is not trapable while it is moving through a fencerow. For instance, the fast-moving 687/688 travelled a minimum of 180 m, 740 m and 480 m on successive days. Certainly it

was not moving on its home range, although the 480 m movement was probably just back along the route which it had already taken. Middleton (1979) has attributed his lack of captures of Peromyscus leucopus in fencerows through which animals apparently moved to the behavior of the animals while moving. Such animals would be surrounded by new and unfamiliar stimuli and would not investigate a trap as thoroughly as would a resident animal, to whom the trap would be a new object in an otherwise familiar area. Many of the chipmunks caught in the fencerows surrounding wood 3 and also in the woodlot were caught at widely divergent points over short periods of time. Hence there is no reason to believe that the same behavior is operative in chipmunks.

The evidence does not support an hypothesis that the dispersion of chipmunks in fencerows is strongly influenced by the distribution of food species. Firstly, the diet of chipmunks throughout the summer is not well known. The work of Krazen and Svendsen (1978) in Ohio indicated a dependence on invertebrates and fungi rather than plant material through the bulk of the summer. This may be the case here as well, since the mast-producing species of trees were not producing in midsummer. An exception is red maple but it was virtually nonexistent in these fencerows. Strawberries (Fragaria sp) were producing fruit but the quantities involved were extremely

small. Raspberries (Rubus sp.) and gooseberries (Ribes sp.) were producing fruit which may have been used, but were not positively correlated with the presence of chipmunks, at least not according to Pearson's product-moment correlation coefficient. The nonparametric tests which were employed, namely Spearman's and Kendall's coefficients of rank correlation, did show both these species to be positively correlated to chipmunk captures (Table 7). The interpretation of the differences in the results provided by these three tests is difficult. Kendall's and Spearman's tests gave virtually identical results. These nonparametric statistics often lose effectiveness when the data have a lot of "ties" in them, namely many values of either variable which are equal to one another (Nie et al. 1970). The many trapping locations which had zero captures would all be ties and impossible to rank in any order. Also Pearson's product-moment correlation coefficient is most effective when applied to bivariate normal data (Sokal and Rohlf 1969). This assumption may have been violated with varying degrees of severity in some of these tests also.

Seeds of prickly ash (Zanthoxylum) are used by chipmunks, as shown by field observations. Twice in August the round, black seeds were noticed in traps after being carried there by chipmunks. The importance of these seeds in the diet is probably small since they all drop

from the bushes over a very short period in mid- to late-August. Also, the plant is known to contain a lemon-scented volatile oil reputed to have analgesic properties. Thus the palatability of the seeds may be low. The temporal distribution of seeds would insure that chipmunks would not be recorded as being positively correlated to Zanthoxylum anyway.

Both basswood and hawthorn (Crataegus sp) were positively correlated with chipmunk frequency and may produce food which is useful to these animals. However, basswood mast is not likely to be important as a food source until fall. The predominately spring-born chipmunks caught in these fencerows would not have had experience using basswood seeds. The reason for this positive correlation, then, is not clear. Similarly it is not clear why chipmunks would be positively associated with Arctium sp. or Bidens sp. Hawthorn, however, produces fruit which may be available through midsummer. It seems that most of the correlations may well be due to a similar response on the part of both chipmunks and plants to similar local environmental circumstances, rather than due to a direct interaction between the plants and the chipmunks.

Chipmunks and zoogeography

Having thus far described some of the characteristics

of the populations present on this study area one must ask to what extent island biogeographic theory provides a useful conceptual framework in describing these processes. In particular, what can a study done on a single species show with respect to the MacArthur-Wilson theory which was designed to model the relationships between species number, the area of an island and its isolation? First of all, as in all applications of this theory to insular habitats on continents, one must demonstrate isolation. Studies dealing with faunas often assume that the degree of isolation is a linear function of the distance between a source of immigrants and the island in question. This assumption is seldom tested since the ecology of component species involved is poorly understood and can't be properly worked out for each individual case (Henebry and Cairns 1980, Simberloff and Abele 1976a, Simberloff 1978). Although species in a fauna might be assumed to have similar immigration abilities, realistically the degree of isolation will vary depending on the size and mobility of the organisms involved (Daugherty et al. 1978, Cliwicz 1980). The chipmunks studied here are excellent colonizers, considering the scale of distances and the mobility of the animals in both hedgerows and even more open, grassy areas. Of the two recolonizations which were observed in the woodlots subject to removal trapping, wood 2 had immigrants in less than a month and wood 1 had

immigrants in less than two months. The pattern of interchange of individuals between woods 3, 4 and 5 indicated that movement between these areas was a process which went on at a low frequency over the entire summer following emergence of the spring litter. No drop-off in rate of movement that could be due to an effect of distance was observed. Rather, rate of movement was increased tremendously by the presence of brushy fencerows. This obviously important effect of the habitat largely obviates any supposition that the difficulty of crossing an area is a simple linear function of distance (Diamond 1975a, Oxley et al. 1974).

Island biogeographic theory has, as a major tenet, the assertion that the number of species on a particular island will be governed by the opposing forces of immigration and extinction (MacArthur and Wilson 1967). Acting in concert, these two forces cause the turnover of species with the passage of time. Turnover may be defined as an immigration or extinction occurring in the course of the year, usually from one breeding season to the next (Diamond 1975b, Reed 1980). Breeding of a species is usually a prerequisite for inclusion in the biotic community of an area. Various authors have not adopted this viewpoint since breeding often cannot be confirmed (Simberloff 1978, Smith 1975).

In the case of chipmunks, young animals which

immigrated would breed the following year as occurred in woods 4 and 5 in 1979-80. Young individuals also found their way to woods 1 and 2 following the experimental extirpations of 1980. Natural extinctions also took place since only one male chipmunk remained in wood 2 in the spring of 1980. Furthermore, the lack of any breeding chipmunks in woods 4 and 5 in 1979 indicates an immigrant population from which a prior local extinction may be inferred. Hence turnover occurred.

Evidence that local extinctions may be caused by predation has been obtained in an area near North Gower 15 km to the west of this study area (Middleton 1979). After capturing chipmunks commonly in May and June of 1978 in a 6.7 ha woodlot, he caught none throughout July, but in August at least one was present. Mr. Prestley who resided on the farm situated immediately adjacent to that woodlot reported that in the summer of 1978 his cat had brought home a chipmunk "roughly every day". This disappearance of chipmunks, then, may be attributed to predation.

Observations made in the course of this study indicated that cats, either feral or apparently moving out from farmsteads, were a common occurrence anywhere on the study area. However, the type of heavy mortality of the sort noted by Middleton never occurred.

When the rates of immigration and extinction very nearly balance one another, the number of species in a

fauna will remain constant over time at some equilibrium level (Diamond 1969, MacArthur and Wilson 1967, Simberloff and Wilson 1969). Since I examined only one species here in detail, the closeness of approach to equilibrium of the system as a whole could only be inferred. The selective cutting in the woods would cause the habitat to change slowly as gaps in the canopy filled in, suggesting that the system was not close to equilibrium.

Since immigration rate is a function solely of distance according to the theory, the characteristics of the source population should not have an influence, although they could, depending on the habitat and the taxa involved (Earbour and Brown 1974, Diamond 1975a, Henebry and Cairns 1980). In this study the sparsely populated woodlots provided emigrants, although most came from the more densely populated wood 3 due to the larger population there. The nature of the source of immigrants, then, cannot be discounted although it was not part of the original formulation of the model developed by MacArthur and Wilson (1967).

The strong tendency of the chipmunks to disperse meant that the probability of recolonization of an empty piece of habitat, whether good or poor, was very high, 100% usually, within a single summer. Certainly the modification of the MacArthur-Wilson model proposed by Brown and Kodric-Brown (1977) is germane in this case.

They have proposed that a "rescue effect" is operative when immigration is rapid. The influx of immigrants could provide a source of new breeders and new genetic material to a small population in danger of disappearing. It would also mask the occurrence of an extinction since in a later survey the species would be recorded as present (Simberloff 1978). This apparently occurred in woods 4 and 5 in 1979. Although animals were present, none was in breeding condition so they must have emerged from natal burrows elsewhere. In the absence of such data on age structure, a local extinction could not have been inferred.

Should the rescue effect be operative and the habitat poor, the individuals found in an area might be considered mere transients. In dealing with such phenomena, the concept of the patch of habitat island may easily become trivial. Smith (1975) points out that the robins in an apple tree become extinct many times each day whenever they fly somewhere else. He recommends that the boundaries of the system under consideration be expanded until extinction becomes rare. In the present study it is impossible to calculate a rate of extinction to bring our effort into line with these recommendations. However, from the observed small populations in wood 2 in 1979 and the similarly small populations in woods 4 and 5 in 1980 it is very easy to see that extinctions might be a fairly

frequent phenomenon in any single woodlot.

In terms of recommendations which might be made for the conservation of natural communities in agricultural areas, one might ask the question, "which is more valuable, a series of small woodlots or a single large one of size equivalent to the sum of the areas of the small woodlots?" In recent years a heated controversy has arisen in the literature over this subject which the evidence accumulated here probably won't settle (Diamond 1976, Gilbert 1980, Simberloff and Abele 1976a, 1976b, Simberloff 1978, Terborgh 1976, Whitcomb et al. 1976). However, the results presented here may be interpreted in the light of the opposing theoretical perspectives.

The contention made by Simberloff and Abele (1976a, 1976b) and Simberloff (1978) that an archipelago of smaller islands might preserve populations of more species than a single island of identical total area arose from their continuing experiments on small islands of red mangrove in Florida Bay. These workers attempted to demonstrate "faunal relaxation" (Diamond 1975b) or reduction in the number of species on an island due to extinction overshadowing immigration for a period. This process would tend to restore equilibrium at a lower species number appropriate to the reduced area. Simberloff employed mangrove islands in which the species number was known and presumed to be in equilibrium

(Simberloff and Wilson 1970). By dividing a larger island up into two or more smaller ones, an archipelago could be created. Although the species number on each individual islet of the archipelago dropped, the species number of the archipelago as a whole rose above the level of the pre-treatment island (Simberloff and Abele 1976a, Simberloff 1978). This was attributed to an ability of some species to find refuges from predators or competitors in some islets of the archipelago while these predators or competitors excluded them from other islets (Simberloff 1978). On the basis of this evidence, they challenged the heretofore generally accepted theory that a larger island would always be more useful than one or a few smaller islands since it would maintain a higher equilibrium number of species (Diamond 1975b, Wilson and Willis 1975). This was not taken lightly and the countercharge was made that should a large area be fragmented into smaller pieces, those species which would go extinct first would be those most dependent on undisturbed habitat such as deep forest or climax vegetation and hence would be the most needful of protection (Diamond 1976, Terborgh 1976, Whitcomb et al. 1976).

Which of these alternatives would be more useful in preserving the most complex possible deciduous woodland community is not clear as yet. As far as the chipmunks and perhaps some other small mammals are concerned, a

local extinction would not be of great import, since recolonization from the other surrounding woods would occur. Fragmented woods possess more edge, which may benefit chipmunks and perhaps other small mammals and birds (Forsyth and Smith 1973, Heliwell 1976, Ranney 1977). The decision of the landscape manager might be different if small birds typically found in deep forest are of paramount consideration (Diamond 1978, Terborgh 1976, Whitcomb et al. 1979).

An alternative conceptual model of this series of woodlots is the patch dynamic model which suggests that the size and distribution of patches can have considerable importance as a stabilizing factor for populations living in a heterogenous environment (Hassell 1980, Lomnicki 1980, Roff 1974a, 1974b, 1975). In fact, patches possessing insularity sufficient that they might be considered islands can be considered as showing a very extreme type of habitat heterogeneity (Pickett and Thompson 1978, Stenseth 1980). The patterns of disturbance followed by succession (given that the land doesn't become a farmer's field) will result in a series of patches of varying quality distributed over the landscape. In view of the ability of chipmunks to use fencerows as travel routes and occasionally as breeding habitat, it appears that the chipmunks are very capable of finding and exploiting favorable patches. With a number

of patches, the probability of extinction in all patches at once is much reduced.

The overriding importance of area as a predictor of the probability of extinction in an "island" in the conception advanced by the MacArthur-Wilson school has been shown to be less than adequate by many studies which have sought to test this particular tenet (Aho 1978a, 1978b, Barbour and Brown 1974, Dueser and Brown 1980, Heliwell 1976, Johnson and Raven 1973, Simberloff and Abele 1976a, 1976b). In addition to patch area, the contribution of patch quality, including its previous history of disturbance and succession is of central importance in patch dynamic theory (Pickett and Thompson 1978). Unfortunately, most treatments of patch dynamics and heterogeneity are of a theoretical nature and are not currently useful due to the difficulties in quantifying such real world variables as disturbance regime and distribution of patches (both spatially and temporally), the mobility of species and their various habitat requirements. The interaction between a species and the disturbance regime will be the major influence on longevity of a species in a particular system (Simberloff and Abele 1976a, 1976b).

Pickett and Thompson (1978) introduced the concept of "minimum dynamic area" and defined it as "the smallest area with a natural disturbance regime which maintains

internal recolonization sources, and hence minimizes extinction". They also employed this concept in formulating recommendations for the design of nature preserves in a fashion entirely analogous to the efforts made along these lines by the island biogeographers (Diamond 1975b, Wilson and Willis 1975). The major difference in the recommendations is that the patch dynamic viewpoint requires an understanding of the spatial and temporal changes occurring in the various patches in the area to be included in the reserve. As such it is intuitively more satisfying than an island biogeographic point of view which in its original formulation as presented by MacArthur and Wilson (1967) embodied many tenets which have since been shown to be oversimplifications, or at best poorly substantiated as yet (Gilbert 1980). The patch dynamic concept, while still in its infancy insofar as application to natural systems is concerned is likely to be the conceptual framework which will, in the future, answer questions regarding the changes in abundance of species (Hansson 1979). Obviously, a "minimum dynamic area" for chipmunks would include several woodlots of a type seen here. The useful application of this theory to other species will await a more detailed knowledge of both natural history and landscape heterogeneity.

CONCLUSIONS

1. No part of the study area was sufficiently isolated so that it did not receive immigrants from other parts of the area within one year.
2. Chipmunks commonly enter, travel along and reside in fencerows.
3. Where overwintering is possible breeding in fencerows may also occur.
4. The presence of well-developed fencerows containing woody cover or rocks is not required to allow movement between areas of habitat. Movements of at least 0.5 to 1 km will occur over grassy areas.
5. The presence of a population of resident territorial adults is not necessary to cause young animals to emigrate from a habitat isolate. The stimuli for such movements are currently unknown.
6. Chipmunks moving across woodlot boundaries or into areas of fencerows not inhabited by breeding females were almost exclusively young, non-reproductive animals. The few movements of adult males across woodlot boundaries were very short distance movements and appeared to result from adult males occupying home ranges overlapping a section of fencerow and some of the adjacent woodlot.

7. Adult females were never observed to cross woodlot boundaries.
8. The ratio of chipmunks which crossed woodlot boundaries or entered areas of fencerows, not occupied by breeding females was approximately 2:1 (males:females) and this ratio was observed consistently over both years of the study.
9. Local extinctions in these woodlots is a typical feature of the small populations found there. Whether these extinctions are due to the small size of the populations or whether there are compounding effects of habitat in some of the woodlots has not been ascertained.
10. Chipmunk burrow entrances were not in drier soils or on sites at which the soil thawed earlier, but burrow entrances were significantly further from pools of water remaining in the woodlot in the spring than would be expected by chance. Burrow entrances were on mounds more commonly than in intermediate areas or depressions.
11. Chipmunks were more frequently trapped in fencerows having greater cover of rocks, rails, hawthorn (Crataegus sp.), nannyberry (Viburnum lentago) and several other herb species which were commonly associated with rocky, open habitat.
12. Chipmunks were less frequently trapped in

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fencerows having greater cover of woody shrubs.

13. The hypothesis that the five woodlots were functioning as "islands" of habitat in the sense of MacArthur and Wilson (1967) can be rejected with reference to chipmunks.

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APPENDIX I

Species composition of woodlots.

Legend: A - abundant; composing a major part of its particular stratum.

C - common; present, easily observed

R - rare; individuals sparsely distributed

Species	Woodlot				
	1	2	3	4	5
<u>Equisetum laevigatum</u>	R	C	R	C	C
<u>Equisetum arvense</u>	C	C	C	C	C
<u>Adiantum pedatum</u> HH			R		R
<u>Matteuccia struthiopteris</u>	A	C	A	C	A
<u>Onoclea sensibilis</u>	C	R	C	R	R
<u>Athyrium pycnocarpon</u>					R
<u>Athyrium felix-femina</u>	C	C	C	C	C
<u>Gymnocarpium dryopteris</u>	C				
<u>Dryopteris spinulosa</u>	C	C	C	C	C
<u>Polystichum acrostichoides</u>	R		R		R
<u>Abies balsamea</u>	C				
<u>Tsuga canadensis</u>	C				
<u>Thuja occidentalis</u>	R	R			
Grass	C	C	C	C	C
<u>Carex</u> spp.	C	C	C	C	C
<u>Arisaema triphyllum</u>	C	R	C		R
<u>Allium tricoccum</u>	C	C	C	R	C

Species	Woodlot				
	1	2	3	4	5
<u>Erythronium americanum</u>	C				
<u>Uvularia perfoliata</u>	R		R		
<u>Polygonatum biflorum</u>	C	R	C	R	C
<u>Trillium grandiflorum</u>	R	R	C		R
<u>Trillium erectum</u>	R	R	C		C
<u>Populus tremuloides</u>			R	C	
<u>Salix</u> spp.				C	
<u>Juglans cinerea</u>	R				R
<u>Carya cordiformis</u>	R	R	C		R
<u>Carpinus caroliniana</u>	R	R	R		R
<u>Ostrya virginiana</u>	R	B	R	R	R
<u>Betula allenghaniensis</u>	R	R	R	R	R
<u>Fagus grandifolia</u>	C	C	C		C
<u>Quercus macrocarpa</u>	R	C	R	A	R
<u>Ulmus americana</u>			R		
<u>Urtica dioica</u>	C	C	C	C	C
<u>Asarum canadense</u>	C	C	C	R	C
<u>Actaea rubra</u>	R	R	R	R	R
<u>Caulophyllum thalictroides</u>	R		R		C
<u>Menispermum canadense</u>	R	R	R		R
<u>Dicentra cucullaria</u>			R		R
<u>Mitella diphylla</u>	A	A	A	C	A
<u>Ribes</u> spp.	C	C	C	C	C
<u>Spiraea latifolia</u>				C	

Species	Woodlot				
	1	2	3	4	5
<u>Zanthoxylum americanum</u>	C	A	A	A	C
<u>Rhus radicans</u>	C	C	C	C	C
<u>Acer saccharum</u>	R	R	C		C
<u>Acer rubrum</u>	C	A	C	C	C
<u>Acer negundo</u>	C	C	R	R	R
<u>Impatiens biflora</u> ----	A	R	C	R	R
<u>Vitis riparia</u>	C	C	C	C	C
<u>Parthenocissus quinquefolia</u>	C	C	C	C	C
<u>Tilia americana</u>	C	C	C	C	C
<u>Viola pubescens</u>	C	A	C	C	C
<u>Viola rostrata</u>	C	C	C	C	C
<u>Circaea quadrisculata</u>	R		R		R
<u>Sanicula gregaria</u>	C	C	C	C	C
<u>Cryptotaenia canadensis</u>	R		R		R
<u>Osmorhiza claytoni</u>	C	C	C	C	C
<u>Fraxinus americana</u>	C	C	C	C	C
<u>Fraxinus nigra</u>	C	R	C	C	C
<u>Hydrophyllum virginianum</u>	A	A	A	A	A
<u>Galeopsis tetrahit</u>	R	R	R	C	R
<u>Lycopus americanus</u>			R		
<u>Solanum dulcamara</u>	R	R	R	R	R
<u>Solidago flexicaulis</u>			R		R
<u>Eupatorium rugosum</u>	R	R	R		C
<u>Arctium minus</u>	R	R	R	R	R

APPENDIX II

Trapping schedule 1979

	1st trapping period	2nd trapping period
Wood 1	25 May-29 May	22 July-26 July
Wood 2	31 May-7 June	27 July-31 July
Wood 3	11 June-28 June	3 August-12 August
Wood 4	11 July-16 July	18 August-22 August
Wood 5	17 July-21 July	24 August-28 August
Fencerows	27 June-12 July	13 August-17 August

Trapping schedule 1980

	1st trapping period	2nd trapping period
Wood 1	15 May-27 May	17 June-21 June
Wood 2	17 May-27 May	20 June-26 June
Wood 3	3 June-13 June	29 June-9 July
Wood 4	13 June-16 June	7 July-11 July
Wood 5	15 June 19 June	10 July-18 July
Fencerows	28 May-6 June	23 June-1 July
	3rd trapping period	4th trapping period
Wood 1	15 July-19 July	9 August-13 August
Wood 2	19 July-23 July	9 August-13 August
Wood 3	25 July-3 August	3 September-8 September
Wood 4	4 August-8 August	8 September-12 September
Wood 5	4 August-8 August	10 September-14 September
Fencerows	20 July-28 July	14 August-18 August

END

0 1 H 0 9 H 8 2

FIN