

A study of the temporal and spatial relationships
between small-mammals and the immature
stages (larvae and nymphs) of the American
dog tick, Dermacentor variabilis (Say)
(Acari:Ixodidae) in an Aspen Parkland region
near Birds Hill Park, Manitoba

A Thesis

Submitted to the Faculty
of Graduate Studies
The University of Manitoba

By

Vladimyr Ivan Burachynsky

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Requirements for the Degree of
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Department of Entomology

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A STUDY OF THE TEMPORAL AND SPATIAL RELATIONSHIPS
BETWEEN SMALL-MAMMALS AND THE IMMATURE
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(ACARI:IXODIDAE) IN AN ASPEN PARKLAND REGION
NEAR BIRDS HILL PARK, MANITOBA

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VLADIMYR IVAN BURACHYNSKY

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ABSTRACT

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A study of the temporal and spatial relationships between small-mammals and the immature stages (larvae and nymphs) of the American dog tick, Dermacentor variabilis (Say) (Acari:Ixodidae) in an Aspen Parkland region near Birds Hill Park, Manitoba.

During a two year study on the relationships between small-mammals and D. variabilis larvae and nymphs, 739 captures of 427 individual animals were examined for ticks. Captures represented eleven species of mammals: Clethrionomys gapperi (Vigors), Lepus americanus Erxleben, Microtus pennsylvanicus (Ord), Mus musculus Linnaeus, Peromyscus maniculatus (Wagner), Sorex cinerius Kerr, Spermophilus franklinii (Sabine), Spermophilus tridecemlineatus (Mitchell), Tamias striatus (Linnaeus), Tamiasciurus hudsonicus (Erxleben) and Zapus hudsonius (Zimmerman). The most frequently captured species were C. gapperi, M. pennsylvanicus, P. maniculatus, S. franklinii and Z. hudsonius, and except for S. franklinii were also the most frequently infested with larvae and nymphs. The dominant host of D. variabilis larvae and nymphs was the red-backed vole, C. gapperi which produced 42.6% and 60.5% of all larvae collected in 1979 and 1980 respectively, and over 85% of all nymphs collected during both years.

Peak larval activity occurred between the last week of May and the middle of June and peak nymphal activity occurred in July. Peaks were four to five weeks apart.

C. gapperi populations fluctuated as a result of reproductive cycles.

Three periods of recruitment and subsequent population turnover were observed annually. Cycles represented new generations of voles, the beginning of each marked by greater proportions of immatures. Cycles were six weeks apart and roughly coincident with gestation and weaning periods as well as with the period between larval and nymphal activity peaks. Cycle peaks were two weeks earlier in 1980.

First cycle voles were predominantly infested with larvae, and individuals from the second cycle were infested with nymphs. Individuals caught between the two cycles infrequently carried small numbers of both larvae and nymphs. Third cycle voles were very rarely infested.

The area occupied by C. gapperi expanded during each cycle. In 1980, many individuals of the second and third cycles occupied sites outside of the preferred forest habitat. Several second cycle dispersers were infested with nymphs.

Larvae were spatially aggregated during both years. Larvae infested between 10 and 20% of the host population. Location of aggregates varied from year to year.

Nymphal aggregation was not as great as for larval aggregation. The distribution of nymphs overlapped that of larvae each year and occupied a greater area. The distribution of nymphs was highly correlated to that of C. gapperi. The prevalence of nymphal infestations in the C. gapperi population was always higher than for larval infestations. The intensity of nymphal infestations was similar to or less than that for larval infestations.

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DEDICATION

I would like to dedicate this thesis to my father, Roman Burachynsky , for having taught me the importance of knowledge above all things and to my uncle , Dmytro Negrych , who taught me that the love of nature requires discipline before it can lead to understanding.

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INTRODUCTION

Review of pertinent literature

The American dog tick, Derma-centor variabilis (Say), has aroused a great deal of interest during the last two decades in the eastern United States, where the incidence of Rocky Mountain spotted fever has steadily increased since 1958 (Burgdorfer 1975). This disease was formerly considered limited to the mountain areas of North America within the range of the vector, Derma-centor andersoni (Stiles). However, D. variabilis is now the most important vector of Rocky Mountain spotted fever in eastern and southeastern United States and the most likely to attack human beings (Burgdorfer 1975).

In Canada, D. variabilis has been reported from Nova Scotia (Hall and McKiel 1961; Dodds et al. 1969; Garvie et al. 1978), southern Ontario (Sholten 1977), Manitoba and Saskatchewan (Hearle 1938; Gregson 1956; Wilkinson 1967; Gkoroba 1980). The threat of this tick transmitting R.M.S.F. in Canada is evident with the discovery of positive sera from animals and humans (Newhouse et al. 1964; Campbell 1979) and a human case of the disease in Ottawa (Mackenzie et al. 1979).

Several major studies on the ecology and seasonal dynamics of D. variabilis have been conducted during the last twenty years along the eastern seaboard in Virginia (Sonenshine et al. 1966), Massachusetts (McEnroe 1974) and Nova Scotia (Garvie et al. 1978; Campbell 1979). Gkoroba (1980) conducted the first ecological study of D. variabilis in western Canada, the only one prior to this study.

Sonenshine et al. (1966) published the results of the most intensive

study on D. variabilis ecology up to that time. Their study was conducted at Montpelier, Virginia, over a period of three years. They found that larval activity began between March and April and declined to low levels in July, but small numbers were collected in August. Larvae were most frequently collected from small rodents. The peak abundance of nymphs occurred in May with an occasional peak occurring in late August and September following the second larval activity period. Nymphs were most frequently collected from small rodents. They concluded that the activity was bimodal for the two life-stages and that this was indicative of two distinct generations in a season (Sonenshine et al. 1966). The spring larval peak was composed of overwintered individuals while the summer larval peak was composed of individuals hatched the same summer (Sonenshine et al. 1966).

In 1968, Sonenshine and Stout published an analysis of the distribution of adult and immature stages of D. variabilis. The distribution of immature ticks was not correlated with host population densities. Hosts captured within the ecotone areas, dominated by woody shrubs, were more heavily infested with immature ticks than hosts caught in old fields or forest areas. The distribution of immature D. variabilis was positively correlated with habitats dominated by low, woody-deciduous vegetation (ecotone) (Sonenshine and Stout 1968). In addition they observed reduced hatch of D. variabilis eggs at R.H. <65%, and concluded that higher relative humidity in the ecotone and forests regions favoured survival more than in the old fields. Adult D. variabilis were observed to have a distribution different than that of immatures and apparently independent of conditions in the fields (Sonenshine and Stout 1968).

Sonenshine and Levy (1972) studied the distribution of immature and adult ticks in relation to vegetation types in greater detail. The capture frequency of immatures was highly aggregated in the old field-forest ecotone. Adult ticks were less aggregated than the immatures, though most frequently collected in the ecotone.

McEnroe and McEnroe (1973) and McEnroe (1974) observed that adult activity was bimodal in the drier, warmer regions of Massachusetts and unimodal in coastal areas and concluded that relative humidity and mean winter temperatures controlled seasonal activity and survival. McEnroe (1975) suggested that in areas where host populations are relatively stable overwinter mortality is the most important population regulator for ticks. McEnroe (1978a) reported that the distribution of D. variabilis in Massachusetts was limited by the average 0°C winter (Dec., Jan., Feb.) isotherm.

Sonenshine (1979) suggested that the proposed climatic limitations of temperature and relative humidity did not apply to D. variabilis populations in western United States and Canada, some of which were recorded from prairie localities. He concluded his report with a recommendation for further study in this area of tick biology (Sonenshine 1979).

In Nova Scotia, D. variabilis was apparently introduced from the United States in the 1940's (Hall and McKiel 1961) and concern over the introduction of R.M.S.F. was raised. Dodds et al. (1969) reported that the range of this tick in Nova Scotia was expanding.

In 1973 a five year study on the field ecology and seasonal dynamics of D. variabilis was initiated in Nova Scotia by Garvie et al.

(1978). The range had increased since the work of Dodds et al. (1969) in spite of sub zero winter mean temperatures. The seasonal activity patterns of adults and nymphs were unimodal and larval activity was unimodal but occasionally bimodal. Larvae were most abundant in the forest habitats while nymphs and adults were most abundant in the field and ecotone areas (Campbell and McKay 1979).

In 1977, Gkoroba (1980) began a two year study on the field ecology and seasonal dynamics of D. variabilis in Manitoba, at Delta Marsh. He found that seasonal activity of all three life-stages was unimodal and that the abundance of both immature stages was highest in the forest while adults were most common in the ecotone and field.

The dominant hosts of immature ticks differ from study to study. The principal hosts were Peromyscus leucopus (Rafinesque) (Sonenshine 1972), Microtus pennsylvanicus (Ord) (Sonenshine et al. 1966; Campbell and MacKay 1979), Clethrionomys gapperi (Vigors) (Gkoroba 1980) and Peromyscus maniculatus (Wagner) (Stout 1978).

The seasonal dynamics and habitat associations of D. variabilis appear to be only slightly less variable than the dominant hosts of immature ticks. Sonenshine (1972) postulated a one year life cycle in Virginia, McEnroe (1975) a two year life cycle in Massachusetts, Garvie et al. (1978) a two to three year cycle in Nova Scotia and Gkoroba (1980) a two year cycle in Manitoba.

Historical review of Dermacentor variabilis (Say) in Manitoba

The earliest record of a problem with ticks in Manitoba is found in the journal of the famed explorer-fur trader, Alexander Henry. In

1801 he wrote in his journal that,

"Ever since April 25th we have been plagued with wood ticks (a species of *Ixodes*); and now that we are daily in the woods and grass, our clothes swarm with those troublesome and dangerous insects, which often get into the ear and cause inflammation. When they have time to get firm hold they cannot be removed without pulling the body from the head, which remains in the skin, and causes an itching which may last for several months. The bellies of our horses and dogs are covered with them; they adhere to the flesh until they have sucked themselves full of blood and are swelled nearly to the size of a musket ball, when they fall off of themselves. Their natural size is about that of a grain of barley, and in shape they are perfectly flat, with a tough, hard skin, of a chestnut colour. They continue to the end of July, when they suddenly disappear".¹

In 1803, Henry was again beset by ticks while travelling from Fort Pembina to Portage la Prairie in late May,

"May 24th ... we camped; no wood; mosquitoes by the millions, and wood ticks" and then two days later he wrote "Camped at the beaver dam; wood ticks, mosquitoes, rain, and no covering".¹

In 1910 Norman Criddle collected specimens of a tick identified as *D. variabilis* from Aweme, Manitoba (Hewitt 1915). Hewitt at this time reported that Criddle was engaged in limited research on the natural

¹From Elliot Coues (1897), The manuscript journals of Alexander Henry and David Thompson 1799-1814. Published by Ross and Haines, Minneapolis.

history of this tick. Criddle found that the peak of adult activity occurred in June and that the earliest captured specimens were taken on May 25th and the latest on July 17th, a much shorter season than reported by Henry over a 100 years earlier (Hewitt 1915). Dr. S. Hadwen attempted in 1910 to rear D. variabilis through its various life stages on rabbits, succeeding in 1911 and 1912. From these results he constructed the first life table for the species (Hewitt 1915).

In 1938 D. variabilis was reported to be abundant in Manitoba, parts of Saskatchewan and a few districts in Ontario (Hearle 1938). By 1950 the mention of D. variabilis in Manitoba dwindled to one record of two female specimens from an unknown contributor (Gregson 1956), though reports from Nova Scotia, Ontario and Saskatchewan were on the increase. By 1961 the only species of tick mentioned in R.D. Bird's Ecology of the Aspen Parkland was the winter moose tick, Dermacentor albipictus (Packard). However Wilkinson (1967) indicated, on a distribution map of D. variabilis for western Canada, ten records in Manitoba from as far north as Dauphin.

In 1977 Gkoroba (1980) began the first intensive field study on the ecology of D. variabilis in western Canada with observations on host preferences, seasonal dynamics and habitat preferences. In addition he estimated that adult D. variabilis population densities were 36,000 and 148,000 per acre in 1977 and 1978, respectively.

In 1978 a suspected case of D. variabilis induced paralysis of a horse was diagnosed at Virden, Manitoba (J.R. Allen, pers. comm.). Since that time a survey of rural veterinarians conducted by the author revealed that several veterinarians from across the province had diagnosed tick-induced paralysis in horses. In 1979 the author began studies on

D. variabilis ecology at Birds Hill Park, Manitoba.

Objectives

This study was initiated in response to several factors: a) the only other ecological study conducted in the province was in an area of marsh land and river bottom lands while the majority of complaints by rural and suburban residents come from the drier Aspen Parklands, b) unconfirmed reports of tick paralysis were beginning to come to our attention from veterinarians and farmers, c) the alarming increase of R.M.S.F. cases in the United States associated with D. variabilis and the high numbers of this species in Manitoba made us aware of the shortage of ecological data pertaining to Manitoba and d) the inconsistencies between the various ecological studies described earlier pointed out the need for more work in Manitoba.

The objectives of this study were: a) to determine the seasonal dynamics of D. variabilis immatures in an area of the province typical of the dominant forest region, the Aspen Parkland, b) to determine the host species infested by immature D. variabilis, c) to determine the distribution of tick populations with respect to vegetation and hosts, d) to examine dispersal of immature stages, and e) to examine temporal relationships between populations of immature ticks and host populations.

MATERIALS AND METHODS

General description of research plots

An area of land adjoining the southern boundary of Birds Hill Provincial Park (Fig. 1) was chosen as the site of two research plots. This area lies within the Aspen-Oak forest region as described by Rowe (1977).

Trembling aspen was the dominant tree species occurring in continuous and patchy stands, interspersed by prairie grasslands. Bur oak was sporadically dispersed within the dominant aspen stands. Aspen within the continuous stands grows to a greater height than aspen within patchy stands which tends to be quite shrubby (Rowe 1977).

The soils of this area are classified as members of the Leary series of well to excessively well drained Dark Grey soils (Degraded Chernozemic soils). Leary soils have developed on coarse, gravel beach and glacial outwash deposits. Commonly a thin sandy surface covers the coarser materials. The topography is level to very gently sloping. Soil permeability is rapid to very rapid resulting in low moisture retention (Canada-Manitoba Soil Survey 1975).

Plot one dimensions were 120m x 120m while plot two was 80m x 180m; both covered an area of 1.44 ha (3.6 acres).

The two plots, 400m apart, were oriented within this area to include the three major habitat types within their boundaries: forest, field and ecotone (Fig. 2). Habitats were mapped by visually evaluating vegetation type from each trap station on both plots. Habitat boundaries were mapped by pacing with a compass in addition to aerial photo interpretation of vegetation patterns.

The criteria for making habitat distinctions were based on the dominant vegetation characteristics. The field habitat was dominated by grasses and was free of trees and shrubs higher than .75m. The forest habitat was dominated by trees up to 10m in height. The forest floor was virtually free of grasses, due in part to the large amount of leaf litter and low light levels. The ecotone was dominated by shrubs and bushes up to 3m in height. Many woodland and field herbs and grasses were found in the ecotone.

Plant species lists for the two plots were basically similar, but plot two harbored a few species of orchids not seen on plot one. Plot two included some small areas, within the forest, that had a very dense canopy and deep leaf litter. See Appendix I for a complete list of plant species.

Trapping schedule

Plot one was staked out into a 7 station by 7 station grid and plot two into a 10 station by 5 station grid. Stations were 20m apart and a 3" x 3" x 10" live trap (Fig. 3), model no. 101, manufactured by the Tomahawk Live Trap Co. of Tomahawk, Wisconsin, was placed within 2m of the stake adjacent to any suitable cover or runway. One trap site, 9B, on plot two fell in the middle of a road and was abandoned resulting in 49 traps per plot. Occasionally a 6" x 6" x 19" live trap, Tomahawk model no. 202, was placed next to the smaller model to divert trap addicted ground squirrels whenever they were becoming a problem with the small traps.

Traps were set between 7:00 AM and 10:00 AM on two consecutive days every week on each plot. Traps were examined 24 hours later, captures

removed, traps scraped clean, bait replenished and the trap reset.

In 1979 trapping on plots one and two began on 8 and 17 May respectively and continued biweekly until 8 June and then once weekly until 7 September when all trapping ceased. In 1980 trapping on plots one and two began on 23 April and 1 May respectively, and continued biweekly on both plots until 22 August when all trapping ceased. If inclement weather posed a threat traps were closed and the schedule resumed normally when weather improved.

Traps were baited with rolled oats and peanut butter; carrots were added during hot weather to provide a source of water. Traps were covered by a shelter made of two pieces of 1/8" pressed board to provide protection from sun and rain (Fig. 3).

Mammal handling

All animals were transported to the laboratory and given food and water. Each animal was anaesthetized with ether in a large glass container and when unconscious placed on a white enamel tray under strong illumination. Animals were searched for parasites by brushing the pelage vigorously by hand followed by a systematic search of the animals' skin. All parasites were transferred to a vial containing 70% ethyl alcohol, and labelled with the host's capture history, status and background information.

All animals were sexed and given an identification number by clipping toes (Fig. 4). Age, weight and reproductive status were noted and histories of individual rodents compiled including their parasite burdens. When the animal had recovered consciousness it was returned to

a holding cage for the night with a supply of water and food.

Parasites collected from each host-capture were labelled and kept separate from all other material. All material was examined, sorted and processed. Ticks were identified to species and stage of development. Host and parasite data were recombined later using the individual host's date of capture and tag number to insure correspondence.

Animals were returned to the site of capture the next morning and released only after all the traps had been removed from the field. Animals caught over the second 24 hour period were processed in the same manner and returned the following day to the site of capture. Releases were conducted in this manner to avoid trapping the same individual twice in one week.

Rodent population dynamics: recruitment and turnover

To identify periods of population recruitment two criteria were employed. First, the population was monitored for the appearance of juveniles, which were identified on the basis of size and coloration. Secondly, since the juvenile pelage of cricetids (e.g. P. maniculatus) changes quickly to the adult form, a large influx of previously unmarked individuals into a population was taken as a sign of recruitment. When the populations under examination are large, periods of high recruitment are easy to identify. However, at low population densities, these periods are not always obvious. As an indirect method of determining recruitment, population turnover or replacement of individuals was examined. Population recruitment and turnover periods were accepted as having occurred when no individuals

caught before a certain date remained in the population after a later date, even though the population size (M.N.A.) remained constant or increased. Population size was based on the minimum number of individuals known to be alive during a sampling period.

Host population size determination

Population size was estimated using the complete enumeration technique employed by Krebs (1966) and Krebs et al. (1969). By using a computer simulation of M. pennsylvanicus (Ord) populations based on actual data from capture-recapture studies, Hillborn et al. (1976) found that enumerated populations consistently underestimated actual populations by at least 10-20%. Population size was determined for each host species during the present study for two week periods as the minimum number of animals known to be alive or M.N.A. (Mihok 1979; Krebs et al. 1969; Hillborn et al. 1976).

Infestation parameters: Intensity and prevalence

The larval and nymphal infestation parameters of intensity and prevalence were tabulated for each of the host species by month for each plot.

Intensity of infestation is the measure of the average parasite burden of infested hosts,

$$\text{Intensity} = \frac{\text{total number of parasites collected}}{\text{number of infested captures}}$$

unlike the mean infestation which is the average number of parasites per host whether infested or not. Mean infestation figures will not be used in this paper.

Prevalence of infestation is a measure of the proportion of a sampled population infested by parasites,

$$\% \text{ Prevalence} = \frac{\text{number of infested captures}}{\text{total number of captures}} \times 100$$

Indices of dispersion for D. variabilis larval and nymphal distributions

The distribution patterns of D. variabilis larvae and nymphs were tested to determine departure from randomness. This measure is referred to as the index of dispersion by Greig-Smith (1964) and as the coefficient of dispersion by Southwood (1971).

The extent to which the distributions of larvae and nymphs conform to a random or Poisson distribution can be tested by a χ^2 .

$$\chi^2 = \frac{S}{\bar{x}} \times (N-1)$$

where S = variance, N = number of trap sites and \bar{x} = mean number of larvae or nymphs per site. If the χ^2 value calculated lies outside the limits 0.95 and 0.05 of the χ^2 for N-1 (48) degrees of freedom then the distribution is not random. The index of dispersion, $\chi^2 \div (N-1)$ will be approximately equal to one for a random distribution. A value approaching zero is indicative of a regular distribution and a value significantly greater than one, as indicated by a χ^2 value outside of the 0.95 to 0.05 limits, implies an aggregated distribution (Southwood 1971; Greig-Smith 1964; Poole 1974).

Spatial distributions of ticks and hosts

Since there are no practical methods available for sampling free-living larvae or nymphs, the spatial distribution of feeding stages is interpreted from that of infested hosts. This approach, while the only

available, is based on behavioural patterns of hosts and ticks as reported by several researchers in different disciplines.

Tick larvae are thought to remain in discreet clusters on or just above the soil surface (Campbell and McKay 1979; Arthur 1960) until disturbed by a potential host. Dispersal of larvae and nymphs away from the natal site is thought to be restricted to less than two metres (Rechav 1979). While the movements of immature ticks are very limited, the area or territory occupied by the hosts is also restricted indicating that only a certain proportion of a host population has access to any given point in a region. Territory size ranges have been determined for many species of small mammals including those encountered during this study.

The site of an individual rodent's capture was assumed to exist as a point within that animal's home range. If an animal was found to be infested with ticks, it is axiomatic to accept the presence of ticks within the host's territory. The presence of more than one infested host at any point implies a region of overlapping territories with a higher probability of containing ticks than sites free of infested hosts. The relative difference in tick abundance at the various trap sites was assumed to reflect local variations in tick abundance.

The technique of using tick-infested captures to indicate, qualitatively, the distribution of areas with high probabilities of containing ticks is subject to severe limitations. The principle problem is sampling. Rodents sample the tick population and the researcher samples rodents. As a consequence, statements made about the distribution of ticks must be conservative and cautious. Regions devoid of host captures

(i.e. sampling units) are difficult to assess, though there is a tendency to regard individuals within these areas as being functionally isolated from the ongoing processes of tick ecology.

RESULTS

Mammal trapping results (Table 1)

Plot one yielded 229 captures of 105 individual mammals in 1979. Four species, Microtus pennsylvanicus (Ord), Spermophilus franklinii (Sabine), Spermophilus tridecemlineatus (Mitchell) and Zapus hudsonius (Zimmerman), accounted for 92% of the total captures and 87% of the total number of individuals. S. franklinii and S. tridecemlineatus together produced 66% of the total number of captures but only 46% of the individuals, indicating a very high recapture rate. In addition to the four dominant species, three species occurred occasionally: Lepus americanus Erxleben, Clethrionomys gapperi (Vigors) and Tamias striatus (Linnaeus).

In 1980, a dramatic change was observed in the species composition and abundance on plot one. Total captures declined to 122 and total individuals to 82. The number of species captured declined to six. Dominant species were C. gapperi, with 36% of the total captures and 39% of total individuals, and S. franklinii with 40% of the captures and 36% of the individuals. Three of the dominant species from 1979 (M. pennsylvanicus, S. tridecemlineatus and Z. hudsonius) declined in total captures and individuals. C. gapperi captures increased from 8 in 1979 to 42 in 1980. Peromyscus maniculatus (Wagner), absent in 1979, appeared at low levels in 1980.

Plot two yielded 140 captures of 85 individuals in 1979. Ten species were collected in contrast to the seven on plot one (Table 1). The dominant species was C. gapperi, contributing 31% of the total

captures and 33% of total individuals. S. franklinii contributed 21% and 18% to total captures and individuals respectively. P. maniculatus and M. pennsylvanicus contributed together 29% of the total captures. The remaining six species contributed together only 19% of the total captures (Table 1).

In 1980, the total number of captures and individuals increased on plot two (Table 1). The increase in total captures was due, in part, to an increased trapping effort: 17 days in 1979 and 28 in 1980. Fewer days lost to bad weather and additional manpower both contributed to greater trapping effort in 1980.

The four dominant species on plot two in 1980 were C. gapperi, M. pennsylvanicus, P. maniculatus and S. franklinii, which contributed 85% and 82% of the total captures and individuals respectively. The total number of C. gapperi captures increased dramatically in 1980 (Table 1), comprising half of the total number of mammals captured on plot two.

Spatial distributions of small mammals

Plot one 1979

Habitat boundaries were mapped for plot one (Fig. 5) and the vegetation communities of forest, ecotone and field represented approximately 29%, 45% and 26% of the total area respectively.

In 1979 P. maniculatus was absent during the entire season on plot one. C. gapperi appeared at irregular intervals after 21 August from widely separated sites within or adjacent to the forest habitat (Fig. 6a). The forest sites were preferred to ecotone sites by C. gapperi

(Table 2) and the field not at all.

M. pennsylvanicus (Fig. 6b) captures originated from two field and forest sites and ten ecotone sites, and indicated a preference for the ecotone (Table 2). On plot two during this period the majority of M. pennsylvanicus captures came from the field. It appears that in the absence of P. maniculatus and C. gapperi, M. pennsylvanicus will occupy ecotone sites more often than field sites (Table 2).

Z. hudsonius (Fig. 6c), S. franklinii (Fig. 6d) and S. tridecemlineatus (Fig. 7a) distributions all overlapped that of M. pennsylvanicus (Fig. 6b) to some extent. In contrast, M. pennsylvanicus on plot two in 1979 and 1980 (Figs. 10c and 11d) had only P. maniculatus (Figs. 10a and 11b) to contend with over any portion of its range and no ground squirrels.

Z. hudsonius captures were widespread across plot one in 1979 (Fig. 6c), with the majority coming from ecotone sites (Table 2). The field habitat was the least preferred habitat. Individual animals were collected from sites up to 80m apart. Z. hudsonius demonstrated spatial overlap with every other species of rodent known to be present on plot one.

S. franklinii, the dominant species on plot one in 1979, was captured regularly in forest and ecotone habitats but never in the field (Table 2). It occupied 85% of the available forest sites and 72% of the ecotone sites and indicated an overall preference for the forest. The distribution of S. franklinii captures (Fig. 6d) was widespread throughout the forest and ecotone habitats. The apparent aggregations along the western boundary and in the southeast corner (Fig. 6d) do not

reflect high population densities, but rather the high capture rate (3.25) for this species. The aggregates represent stable well used home territories of a few individuals.

The distribution of S. franklinii (Fig. 6d) overlapped that of S. tridecemlineatus (Fig. 7a) peripherally in the ecotone. These two species of sciurids do not normally co-exist since they are most often found in different regions of the province (Banfield 1977). S. franklinii is a common inhabitant of the Aspen Parkland (Bird 1961) forests while S. tridecemlineatus prefers shrubby fields at the edge of prairie grasslands (Banfield 1977).

Captures of S. tridecemlineatus originated primarily from a clearing in the south-central portion of plot one near a small resident colony (Fig. 7a). The majority of captures came from field and ecotone sites while only a few came from forest sites (Table 2).

Plot one 1980

In 1980 the rodent populations underwent dramatic changes in distribution and abundance on plot one. M. pennsylvanicus was captured at only one site in the field and one in the ecotone (Fig. 7b). Three of the four captures came from the field site. This species was the most common myomorph on plot one in 1979 and the least common in 1980 (Table 1).

S. tridecemlineatus, which accounted for 61 captures in 1979, was collected only three times in 1980. The distribution of captures (Fig. 7b) remained within the area occupied in 1979 (Fig. 7a). A combination of unknown factors either displaced or eliminated the majority of the colony formerly residing in the south-central region of the plot. The

large area of land occupied in 1979 surprisingly was not utilized to any extent by the remaining resident species. Hot and dry climatic conditions in 1980 may have rendered the field habitat unproductive or otherwise unsuitable for habitation restricting mammals to the ecotone and forest.

C. gapperi captures increased from 8 in 1979 to 44 in 1980 (Table 1). The majority of captures came from the forest habitat (57%) and the ecotone (36%) while only two field sites (7%) were occupied (Table 2). C. gapperi underwent a great increase in population density on both plots one and two in 1980 and as a result many individuals dispersed into ecotone and field habitats.

The distribution of C. gapperi captures (Fig. 7c) marginally overlapped the distribution of P. maniculatus captures (Fig. 7d), M. pennsylvanicus (Fig. 7b), and S. tridecemlineatus (Fig. 7b). The most extensive overlap occurred between C. gapperi (Fig. 7c) and S. franklinii (Fig. 8b). Z. hudsonius captures (Fig. 8a) frequently came from sites occupied by C. gapperi but repeat captures of Z. hudsonius from those sites were infrequent.

The distribution of Z. hudsonius captures (Fig. 8a) was widespread and diffuse throughout the forest and ecotone (Table 2) with only a single capture coming from a field site. The number of Z. hudsonius captures declined to 15 in 1980 from 28 in 1979 but the distribution of captures in the three habitats was similar (Table 2).

The two areas of high capture frequency to S. franklinii in 1979 (Fig. 6d) remained in approximately the same positions in 1980 (Fig. 8b). The majority of captures, 57%, came from the ecotone while the remainder

came from the forest (Table 2), exactly the opposite of the 1979 distribution (Table 2). Ten of the individuals captured in 1979 were recaptured in 1980 from sites they had previously occupied and three of the ten were recaptured in 1981 (T.D. Galloway, pers. comm.) with little change in their home ranges.

Plot two 1979

The habitat boundaries for plot two were mapped (Fig. 9) and the vegetation communities of forest, ecotone and field represent approximately 55%, 18% and 27% respectively.

P. maniculatus captures on plot two in 1979 were distributed over the ecotone (Fig. 10a) and extended into the adjacent field and forest sites. The ecotone and forest sites were favoured over field sites (Table 2) by a slight margin. Spatial overlap occurred between P. maniculatus and C. gapperi (Fig. 10b), Z. hudsonius (Fig. 10d) and S. franklinii (Fig. 11a) only in the forest habitat. Spatial overlap between P. maniculatus (Fig. 10a) and M. pennsylvanicus (Fig. 10c) was not evident in 1979. Ninety-nine percent of the available ecotone sites were occupied at least once by either P. maniculatus or M. pennsylvanicus without any overlapping of sites. The only other species captures from a site occupied by M. pennsylvanicus was Z. hudsonius (Fig. 10d).

M. pennsylvanicus occupied seven trap sites in two distinct areas of the plot separated by approximately 80m (Fig. 10c). The distribution of captures was entirely restricted to the periphery of the plot and it is probable that a large population of M. pennsylvanicus resided east of the plot in an area of extensive field habitat.

Over 90% of all C. gapperi captures came from the forest habitat (Table 2). All captures from the ecotone came from a single site, 3D, adjacent to the forest on three sides (Fig. 10b). C. gapperi captures were aggregated in the southwest corner of the plot and dispersed in other areas of the forest. The distribution of C. gapperi captures overlapped the distributions of P. maniculatus (Fig. 10a), in areas next to the ecotone, and S. franklinii (Fig. 11a) throughout the forested areas. Z. hudsonius (Fig. 10d) was also captured in forested areas but at only one trap site, 8C, where both Z. hudsonius and C. gapperi were recorded (Fig. 10d). No overlap was observed between C. gapperi and M. pennsylvanicus, during the 1979 season.

Z. hudsonius captures came from all three habitats but the majority, 4 out of a total of 8, came from the ecotone. Only one capture came from a field site (Fig. 10d). Captures of Z. hudsonius came from several sites that were occupied by other species at some time during the season. Spatial overlap occurred between Z. hudsonius and C. gapperi (Fig. 10b), P. maniculatus (Fig. 10a), M. pennsylvanicus (Fig. 10c) and S. franklinii (Fig. 11a).

S. franklinii captures were widely distributed throughout the forest and limited in the ecotone (Fig. 11a). Eighty-six percent of the total captures of S. franklinii (Table 2) came from the forest and 14% from the ecotone. The majority of captures in the forest came from the northwest corner of the plot (Fig. 11a) and smaller numbers from the southwest corner. When the distribution patterns of C. gapperi (Fig. 10b) and S. franklinii (Fig. 11a) are compared it appears that where one species is most

frequently captured the other is not.

Plot two 1980

The distribution of P. maniculatus captures (Fig. 11b) was centred over the ecotone as in 1979 (Fig. 10a) but a greater number of captures came from forest sites. Range expansion into the forest occurred northwards along trap lines 9 and 10, which lie on either side of a forest trail (Fig. 9). A slight reduction in captures from the field and forest sites in the south was noted in 1980 from that of 1979 (Fig. 10a).

The number of sites occupied by both C. gapperi (Fig. 11c) and P. maniculatus (Fig. 11b) was greater in 1980 than in 1979. The number of sites occupied by P. maniculatus and M. pennsylvanicus (Fig. 11d) also increased in 1980. The proportion of the P. maniculatus population captured in the field decreased in 1980 while the proportions caught in the forest and ecotone both increased (Table 2).

The distribution of C. gapperi captures (Fig. 11c) in 1980 on plot two included 96% of the available forest sites (Table 2). The population size of C. gapperi, based on the number of individuals present, increased by roughly 2.5 times between 1979 and 1980 (Table 1). In 1980 the forest was still the most heavily used habitat by C. gapperi (Table 2) but animals were taken in greater numbers from both the ecotone and field habitats. As a consequence C. gapperi captures came from sites in areas formerly the exclusive domain of M. pennsylvanicus (Figs. 10c; 11d) and P. maniculatus (Figs. 10a, 11b).

The distribution of M. pennsylvanicus captures (Fig. 11d) in 1980 was very similar to that of 1979 (Fig. 10c). There was a slight increase

in the capture frequency and the number of sites occupied. The two distinct sub-populations seen in 1979 appeared in the same general areas in 1980. The distance between the populations decreased from 80m in 1979 to 60m in 1980. The size of the northern population remained the same while the number of captures in the southern group increased by a factor of two from 1979. The southern group also increased the size of the area occupied and actually extended into the forest sites, 1D and 2D (Fig. 11d).

The number of Z. hudsonius captures, increased from 8 in 1979 to 14 in 1980 on plot two. The majority of the captures came from forest sites, 68%, and none from the field. The capture frequency per trap site was uniform at one per site (Fig. 12a). Only two of the sites occupied by Z. hudsonius in 1979 (Fig. 10d) were again occupied in 1980 (Fig. 12a). The capture distribution for Z. hudsonius overlapped those of M. pennsylvanicus (Fig. 11d), C. gapperi (Fig. 11c), P. maniculatus (Fig. 11b) and S. franklinii (Fig. 12b). No other species on either plot exhibited such a dynamic distribution pattern and at the same time such a uniform capture frequency.

The distribution of S. franklinii captures (Fig. 12b) in 1980 on plot two was more widespread than in 1979 (Fig. 11a) even though the number of individuals captured remained the same (Table 1). Individuals were captured at higher rates in the ecotone and field areas in 1980 than in 1979 (Table 2). S. franklinii captures overlapped those of P. maniculatus (Fig. 11b), C. gapperi (Fig. 11c), M. pennsylvanicus (Fig. 11d) and Z. hudsonius (Fig. 12a).

Rodent population dynamics

Clethrionomys gapperi (Vigors)

In 1979 there appeared to be three overlapping groups of individuals present for limited periods of time over the season (Fig. 13). The graph of Minimum Number Alive (M.N.A.) reflects a temporary increase in numbers for each of the three groups. The peaks of population numbers were six weeks apart. Since none of the individuals trapped during one peak were known to be alive in the subsequent peak, the C. gapperi population apparently underwent three periods of recruitment and population turnover. Since the first population density peak contained juveniles, the individuals within this group were thought to represent both overwintered animals and their offspring.

In 1980 three peaks of population size were again noted to be six weeks apart (Fig. 14) but advanced by two weeks. The spring of 1980, based on the disappearance of snow, was two to three weeks earlier than in 1979. The first peak occurred between 21 April and 9 June (Figs. 14, 15) and appeared to be composed of two groups of individuals. On the basis of capture histories, no individual caught prior to 12 May was recaptured after 19 May. At the end of May the first confirmed juveniles were captured. The two subgroups of the first population peak appear to be overwintered adults followed by their progeny. A small number of individuals were captured during more than one population peak in 1980 (Fig. 14).

Microtus pennsylvanicus (Ord)

In 1979 there appeared two widely separated peaks of population

size on the M.N.A. graph (Fig. 16). Between the two peaks there was a period of population turnover, based on capture histories, (Fig. 16) and recruitment of another group of individuals. This interpretation was based on the capture of pregnant females prior to 26 May which gave birth in the laboratory.

In 1980 the total number of M. pennsylvanicus captures declined (Table 1). The M.N.A. graph (Fig. 17) of 1980 is similar to that of 1979 (Fig. 16). However there is more overlap between the capture histories of individuals in 1980 (Fig. 17) and this tends to obscure evidence of a population turnover during the early season. A group of recruits, identified at the end of the season, made up the entire population known to be alive at that time. As a consequence the population was assumed to have turned over during July or August (Fig. 17).

Peromyscus maniculatus (Wagner)

P. maniculatus captures were too few (Table 1) and far between in 1979 (Fig. 18) to draw any conclusions about turnover periods. The number of captures in 1980 increased substantially (Table 1) and there appeared to be a turnover and recruitment period in late June (Fig. 19). Another period of recruitment was observed in August. The graphs of M.N.A. were quite stable in both 1979 (Fig. 18) and 1980 (Fig. 19).

Zapus hudsonius (Zimmerman)

In 1979 a major peak of recruitment for Z. hudsonius occurred in late May and early June (Fig. 20). A second minor recruitment episode occurred in late August and early September. Since Z. hudsonius is

reported to be a hibernator (Banfield 1977; Quimby 1951; Whitaker 1963), the first peak of recruitment consisted solely of overwintered adults. The second peak appeared to be associated with juveniles. Population turnover was obscured by the low recapture rates during the late summer. Four individuals caught prior to 21 July were not recaptured until the following year. This suggests that many individuals that disappear from the plot may simply be untrappable not dead.

In 1980 only one period of recruitment of Z. hudsonius was observed (Fig. 21) and that in late May and June associated with the emergence of individuals from hibernation. The four individuals (tag numbers 5, 11, 15 and 22) that were first captured in 1979 (Fig. 20) and again in 1980 (Fig. 21) would have been at least one and a half years old when last seen, if they had hibernated prior to their first capture. The large number of individuals trapped for the first time in 1980 are most likely the product of a 1979 breeding cycle that was not evident from capture data. It appears that juvenile Z. hudsonius were not effectively sampled with the trapping techniques employed in this study.

Spermophilus franklinii (Sabine)

The population of S. franklinii underwent two periods of recruitment (Fig. 22) and population peaks. The first peak was made up entirely of individuals recently emerged from hibernation, and occurred in May and early June. The second peak of recruitment occurred in late July and August and was composed of some adults but primarily juveniles of the year. The disappearance of adults in the late summer was due in part to their entering hibernation (Haggerty 1968). Many of these adults were

recaptured the following spring. Only two of the ten individuals captured as juveniles in 1979 were captured in 1980.

In 1980 the two periods of recruitment of S. franklinii occurred slightly earlier than in 1979 (Fig. 23). The number of juvenile recruits associated with the second period of recruitment was lower than in 1979 but the total number of individuals identified was nearly the same (44 in 1979; 46 in 1980 from Table 1). Population turnover in this species appears to be much slower than for the myomorph species. Two individuals captures for the first time in 1979 (tag numbers 12 and 50) were captured in 1981 and were at least two years old and in the case of tag number 12 possibly three years old when last seen in 1981 (T.D. Galloway, pers. comm.).

Host species contribution to total larvae

A total of 101 larvae were collected in 1979 (Table 3) from both plots, after examining 369 captures of 190 individual animals (Table 1). C. gapperi and M. pennsylvanicus contributed over 90% of all the D. variabilis larvae collected (Table 3). P. maniculatus and Z. hudsonius were the only other species from which larvae were collected in 1979. On the basis of the pooled data roughly the same number of larvae were found on both C. gapperi and M. pennsylvanicus and appeared to be equally important as hosts of larvae. However when both C. gapperi and M. pennsylvanicus were present on the same plot, as was the case on plot two, C. gapperi was the dominant host of larvae (Table 3). On plot one in 1979 C. gapperi was absent during the larval activity period and as a result M. pennsylvanicus was the dominant host. C. gapperi carried 91% of the larvae on plot two while M. pennsylvanicus carried 90% of the

larvae on plot one (Table 3).

In 1980, 86 larvae were collected (Table 3) from 370 captures of 237 individual animals (Table 1). C. gapperi was the dominant host species, contributing 61% of all the D. variabilis larvae collected on both plots. P. maniculatus contributed 21% while M. pennsylvanicus and Z. hudsonius each contributed less than 10%. One larva was collected from S. franklinii on plot two.

C. gapperi was the most important host species overall and on each plot. It contributed 71% of all larvae on plot one and 50% on plot two, considerably less than in the previous year (Table 3). P. maniculatus contributed a greater proportion of larvae on plot two in 1980, 30%, than in 1979, 6% (Table 3). M. pennsylvanicus did not contribute a single D. variabilis larva on plot two. It was the second most important host of larvae on plot one in 1980, contributing 20% of the total collected on that plot after having been the most important host species in 1979 (Table 3).

D. variabilis larval infestation parameters

On plot one in 1979 infestations of larvae on hosts were observed only in June (Table 4) on M. pennsylvanicus and Z. hudsonius. Fifty percent of the M. pennsylvanicus captures for that month were infested at an intensity of 11.7 larvae. Only 10% of the Z. hudsonius captures were infested at an average intensity of 3.0 (Table 4).

On plot two in 1979 larval infestations of hosts were seen in June and July. All four species of myomorphs were infested in June and only C. gapperi in July (Table 4). C. gapperi had the highest intensity of

larval infestation of the four species of myomorphs in June at 9.25. The prevalence of infestation for C. gapperi in June was 29% and in July 27% however the intensity in July was only 2.0.

Larval infestations were most common and severe in June of 1979 on both plots.

In 1980 on plot one C. gapperi was infested with larvae in May, June and July. The three other species of myomorphs, P. maniculatus, M. pennsylvanicus and Z. hudsonius were infested only in June. M. pennsylvanicus had the highest intensity of infestation overall, 8.0, even though the majority of larvae came from C. gapperi (Table 4). The infestation parameters for C. gapperi were highest in May and lowest in July (Table 4).

On plot two in 1980, larval infestations on C. gapperi and P. maniculatus occurred in May, June and July (Table 4). Z. hudsonius, the only other species infested, was infested with larvae only in May, when 3 of the 7 captures were infested at an intensity of 2.0. A single capture of P. maniculatus carried a single larva in May while 25% of the C. gapperi captures were infested with larvae at an intensity of 1.6. In June 35% of the C. gapperi captures were infested at an intensity of 1.8 while 30% of the P. maniculatus captures were infested at an intensity of 3.3. In July single infested captures of C. gapperi and P. maniculatus were infested with 1 and 4 larvae respectively (Table 4).

Infestations of D. variabilis larvae were most common and severe in June of 1980 as they were in 1979 even though infestations were observed over a longer period of time.

Host species contribution to total nymphs collected

In 1979 a total of 53 nymphs were collected from plots one and two after examining 369 captures of 190 individuals (Table 5). D. variabilis nymphs were collected from six species of rodents. C. gapperi contributed 86% of the total nymphs collected, M. pennsylvanicus and P. maniculatus 4% each while Z. hudsonius, S. tridecemlineatus and T. striatus each contributed 2% (Table 5).

Less than 10% of the total nymphs collected in 1979 came from plot one where two nymphs were removed from M. pennsylvanicus and one each from Z. hudsonius and S. tridecemlineatus (Table 5).

On plot two in 1979, 94% of all nymphs collected were removed from C. gapperi. T. striatus produced 2% and P. maniculatus 4% of the nymphs.

In 1980, 182 nymphs were collected on the two plots from four species of rodents. C. gapperi was the most important source of nymphs, contributing 85% of all nymphs collected (Table 5). P. maniculatus was the second most important source, contributing 11% to the total, while T. striatus and Z. hudsonius contributed 1% and 3% of all nymphs collected, respectively. Nymphs were not collected from M. pennsylvanicus nor from the two species of ground squirrels, S. franklinii and S. tridecemlineatus.

On plot one in 1980, C. gapperi produced 86% of all nymphs collected while P. maniculatus and Z. hudsonius yielded 7% each (Table 5).

On plot two in 1980, C. gapperi was the most important source of nymphs, yielding 84% of the total collected. P. maniculatus and T. striatus contributed 14% and 2% of all nymphs, respectively (Table 5).

D. variabilis nymph infestation parameters

Nymphal infestation parameters of intensity and prevalence were tabulated on a monthly basis for the five most important host species on each plot during 1979 and 1980 (Table 6).

On plot one in 1979, nymph-infested hosts were captured in June and July. Two nymphs were removed from a single M. pennsylvanicus and one nymph from Z. hudsonius in June. A single nymph was removed from S. tridecémlineatus in July (Table 6).

On plot two in 1979, nymphs were recovered from C. gapperi in July and August and from P. maniculatus and T. striatus in July only. The prevalence and intensity of nymphal infestations on C. gapperi were both highest in July (Table 6).

In 1980 on plot one, nymph-infested individuals of C. gapperi, P. maniculatus and Z. hudsonius were collected in June and July (Table 6). C. gapperi had a higher prevalence and intensity of nymphal infestation in June than July. Due to the small number of infested captures of P. maniculatus and Z. hudsonius, the prevalence values for these species are highly variable.

On plot two in 1980, infested C. gapperi and P. maniculatus were observed in June and July while infested T. striatus were seen in July only. The prevalence and intensity of nymphal infestations for C. gapperi were nearly identical in June and July while they were highest for P. maniculatus in July. C. gapperi was also infested at low intensities and prevalence in May and August (Table 6).

Seasonal activity of D. variabilis larvae and nymphs

1979

The period of larval activity in 1979 began on 1 June and ended 26 July. Over 90% of the larvae were collected in June. The first nymphs were collected on 26 June and the last on 29 August (Fig. 24). On the basis of biweekly totals of nymphs collected, the peak of activity occurred between the second and third weeks of July when 43% of the total were collected. The peak of nymphal activity followed that of larvae by approximately five weeks (Fig. 24).

1980

In 1980 snow disappeared from the plots in early April and maximum daily temperatures were above 20°C by the middle of the month, unlike 1979 when snow remained on the plots until the middle of May. Trapping in 1980 was initiated two weeks earlier than in 1979 in anticipation of early tick activity.

The first larvae of 1980 were collected on 1 May, a full month earlier than in 1979. The last larvae were collected on 16 July. Approximately 35% of all larvae were collected before 1 June. In spite of the early emergence, the peak of activity coincided with that of 1979, between 1 June and 30 June (Fig. 25).

The first nymphs of 1980 were collected on 29 May and the last on 1 August (Fig. 25). The peak of nymphal activity, based on biweekly collections, occurred between the second and third weeks of July when 50% of all nymphs were collected (Fig. 25). The peaks of larval and nymphal activity were approximately five weeks apart in 1980.

Spatial distribution of D. variabilis immatures

Plot one

The distribution of D. variabilis larvae on plot one in 1979, (Fig. 26a) was highly aggregated with an index of dispersion of 20.79 (χ^2 , 48 d.f., $\alpha = .95$). Four sites, G3, G6, F6 and F2, produced larvae. These sites represent two groups, F6-G6 and F2-G3, separated by approximately 60 metres. Larvae were collected from M. pennsylvanicus at sites G3 and F6 which are both in the ecotone (Fig. 5). Larvae were removed from Z. hudsonius captures at sites, G6 and F2, adjacent to those of larval-infested M. pennsylvanicus captures. The distribution of larvae did not necessarily reflect higher host capture frequencies at various sites. The site where greatest numbers of M. pennsylvanicus were captured was G7 (Fig. 6b). Over 90% of all larvae came from the ecotone sites.

The index of dispersion for the distribution of nymphs in 1979 on plot one was 1.44; not significantly different from random, (χ^2 , 48 d.f., $\alpha = .95$) (Fig. 26b). Site G3 which produced large numbers of larvae (Fig. 26a), produced two nymphs (Fig. 26b) from infested M. pennsylvanicus. Single nymphs were taken from Z. hudsonius at site D7, and from S. tridecemlineatus at site C3. Neither of these two sites had previously produced larvae infested captures.

In 1980 the distribution of larvae on plot one changed dramatically (Fig. 26c) from that of 1979 (Fig. 26a). The index of dispersion was 9.1, significantly different from random and highly aggregated (χ^2 , 48 d.f., $\alpha = .95$). The eight sites from which larvae were collected

in 1980 (Fig. 26c) produced none in 1979 (Fig. 26a). The ecotone sites that produced larvae, B1, C1 and D1 were less than 7 metres from a forest outside of the plot. Site G7 was within a field habitat (see Fig. 5 for habitat boundaries). The forest sites produced 48% of all larvae while the ecotone and field sites produced 33% and 19%, respectively. M. pennsylvanicus carried all the larvae collected at site G7, P. maniculatus at site B1 and Z. hudsonius at site C1. At remaining sites that produced larvae, the host was always C. gapperi.

The index of dispersion for nymphs in 1980 on plot one was 9.0 significantly different from random (χ^2 , 48 d.f., $\alpha = .95$) and highly aggregated. The nymphal index was similar to that of larvae during the same season on this plot. However the distribution pattern for nymphs (Fig. 26d) was considerably more dispersed than that of the larvae (Fig. 26c). Seven out of eight sites which produced larvae also produced nymphs in 1980 (Figs. 26c, 26d). Seven additional sites produced nymphs but no larvae. The distribution of nymphs was wider than that of the larvae but inclusive of it as well. The forest produced 58% of all nymphs while the ecotone and field produced 40% and 2%, respectively.

Z. hudsonius captures from site F5 and D1 were infested with 4 and 1 nymphs, respectively. Also at site D1, 18 nymphs were removed from C. gapperi (Fig. 26d). Three nymphs were removed from a P. maniculatus capture at site G1 and single nymphs from P. maniculatus at sites A1 and B1. Remaining nymphs came from C. gapperi from the remaining sites (Fig. 26d).

Plot two

In 1979, on plot two, the distribution of larvae had an index of dispersion of 12.4, significantly different from random and highly aggregated (χ^2 , 48 d.f., $\alpha = .95$). The greatest number of infested captures, all of C. gapperi, came from a wedge-shaped area between sites 5C, 2E and 5E (Fig. 27a). This area produced 90% of all larvae and lies completely within the forest (Fig. 9). Z. hudsonius yielded larvae at trap site 7A. P. maniculatus and M. pennsylvanicus produced larvae collected from sites 2A and 10B for the former and 10C for the latter.

The distribution of nymphs on plot two in 1979 (Fig. 27b) had an index of dispersion of 9.8 and was highly aggregated (χ^2 , 48 d.f., $\alpha = .95$). Sixty-seven percent of the nymphs came from the same general area that produced the majority of larvae (Figs. 27a; 27b). Nymph-infested captures of P. maniculatus came from sites 8A in the field and 7B in the ecotone (Fig. 9). C. gapperi contributed nymphs recorded from the remaining eight sites all of which were in the forest.

In 1980, the distribution of larvae on plot two (Fig. 27c) had an index of dispersion of 2.8, which indicates an aggregated distribution significantly different from random (χ^2 , 48 d.f., $\alpha = .95$). The distribution pattern of larvae was quite different from that of 1979 (Figs. 27a, 27c). Distinct regions of high numbers of larvae were not discernable in the northern half of the plot (Fig. 27c), due to the wide distribution of the infested captures. In the southwest corner of the plot (Fig. 27c) a number of larvae were removed from C. gapperi captures from sites that also produced larvae in 1979 (Fig. 27a).

At sites 8B and 10B, larvae were removed from both P. maniculatus

and C. gapperi captures. Larvae were also removed from Z. hudsonius captures from sites 10A, 10B and 10E; from P. maniculatus only, at sites 10D and 10E; from C. gapperi only at sites 1E, 2E, 3D, 3E, 4D, 7C, 8C, 8D, 8E, 10C and 10D.

The distribution of nymphs on plot two in 1980 (Fig. 27d) had an index of dispersion of 4.8, significantly different from random and was aggregated (χ^2 , 48 d.f., $\alpha = .95$). Over 80% of all nymphs collected came from C. gapperi captures. Nymphs were removed from P. maniculatus captured at sites 6D, 8B, 9C, 9D and 10C and a single T. striatus capture from site 2C yielded nymphs. C. gapperi were captured infested with nymphs at every trap indicated in Figure 27d with the exception of sites 6D and 8B. Ninety-seven percent of all nymphs collected came from forest sites, with 1% and 2% coming from the field and ecotone, respectively. Twelve of the 23 sites that produced nymphs also produced larvae, in 1980 on plot two (Figs. 27c, 27d).

DISCUSSION

Spatial distribution of D. variabilis larvae and nymphs

In Manitoba, at Birds Hill, the field habitat produced the lowest number of immature ticks annually while the forest produced the highest number over the period 1979 to 1980. Under certain conditions the ecotone produced large numbers of larvae and nymphs. Survival of ticks molting from the larval to nymphal stage appeared to be higher in the forest habitat than in the field or ecotone.

The single most important factor determining the distribution of larvae and nymphs was the myomorph rodent population in an area. The most important species of myomorph was C. gapperi followed by either P. maniculatus or M. pennsylvanicus.

In 1979 on plot one the dominant myomorph rodent during the larval and nymphal activity periods was M. pennsylvanicus since both C. gapperi and P. maniculatus were absent. As a result M. pennsylvanicus was the most important host of D. variabilis larvae and nymphs even though very few nymphs were collected. The ecotone produced over 90% of all the larvae collected, since this was the area occupied by the hosts.

Competition between the various species of myomorphs or lack of it, was an important factor in determining the observed spatial distribution of larvae and nymphs. M. pennsylvanicus is reported to be an inhabitant of open grasslands and meadows (Banfield 1977; Iverson et al. 1967; Iverson and Turner 1973) while C. gapperi prefers mixed deciduous, mixed coniferous and aspen stands (Iverson and Turner 1973). In the absence of competition from C. gapperi, M. pennsylvanicus is capable of occupying forested and shrubby areas (Grant 1970; Cameron 1964; Clough 1964)

as was the case in 1979 on plot one.

In 1980 on plot one C. gapperi numbers increased dramatically and this species became the dominant myomorph occupying forest and ecotone areas. M. pennsylvanicus captures decreased and were primarily limited to field sites. C. gapperi became the dominant host of larvae and nymphs supporting 71% and 86% of the total respectively. Slightly less than half of all the larvae were taken from the forest and one-third from the ecotone. The dramatic increase in the numbers of C. gapperi on plot one in 1980 changed the distribution of larvae from predominantly ecotonal in 1979 to forest in 1980.

In 1979 on plot one very few nymphs were collected when the dominant myomorph was M. pennsylvanicus however in 1980 large numbers of nymphs were removed from C. gapperi. A greater proportion of the nymph population was collected in the forest, than of the preceding larval population. It appears there is a higher probability of larvae surviving to the nymphal stage in the forest than elsewhere. Similar results were obtained on plot two in 1979 and 1980, where the forest-inhabiting C. gapperi supported a larger proportion of the nymphal population than the larval population. Campbell and McKay (1979) found during the course of their field experiments on the life stages of D. variabilis, that the forest and field ecotone habitats were more favourable to tick survival than the field habitat. Campbell and Harris (1979) reported that temperature extremes as encountered in field microhabitats had a detrimental effect on the development of the immature stages.

Mature female ticks appear to oviposit in any of the three habitats

since larvae-infested M. pennsylvanicus were collected at Birds Hill on plot two in 1979 from field sites 60m from the forest. Home ranges of M. pennsylvanicus are reported to be among the smallest of the myomorph species (Banfield 1977), ranging from approximately 30m² to 300m² with the mean for females being 68.6m² and males, 192.3m² (Madison 1980). It is unlikely that infested M. pennsylvanicus in field areas could have ventured into the forest habitat to become infested, especially in the presence of C. gapperi, but rather contacted larvae in the field in the same general area where egg clusters were deposited by females.

A combination of biotic and abiotic factors favours the survival of immature stages of D. variabilis in the forest and ecotone. The distribution of larvae and nymphs within favourable habitats is dependent on the behaviour and biology of the dominant myomorph species during the periods of larval and nymphal activity.

In several studies the distribution of D. variabilis has been related to vegetation types (Sonenshine et al. 1966; Sonenshine and Levy 1972; Campbell and McKay 1979). Some similarities and discrepancies may be due in part to different rodent community structure and composition.

In Virginia all stages of D. variabilis were most frequently collected at or close to ecotonal areas (Sonenshine et al. 1966; Sonenshine and Levy 1972; Sonenshine 1975). The most important host of immature stages in the Virginia studies as determined over the seven year period from 1963 to 1970, was Peromyscus leucopus followed by M. pennsylvanicus (Sonenshine 1975). P. leucopus is reported to be primarily a forest inhabitant (Iverson et al. 1967; Banfield 1977) as is C. gapperi, however P. leucopus appears to have a broader ecological

tolerance since it may occur in grasslands and forb-grass stages of succession (Hirth 1959; Pearson 1959; Wetzel 1958). The difference in the behaviour of the dominant myomorphs in the Montepellier, Virginia and Birds Hill, Manitoba studies may account for the observed difference in distributions of immature ticks with respect to vegetation.

Campbell and McKay (1979) found that larvae were most abundant in forested areas and nymphs in the old fields and ecotone. The myomorph rodent community included P. leucopus, P. maniculatus, C. gapperi, M. pennsylvanicus and Z. hudsonius. C. gapperi was the dominant host of larvae in the forest while Peromyscus spp. carried the most larvae in the ecotone and M. pennsylvanicus the most in the old field. These findings are in accordance with the preferred habitats of each of the three genera of myomorph rodents. In general each of the host species contributed roughly the same proportion to the total number of larvae as nymphs collected except for M. pennsylvanicus which contributed a greater proportion of nymphs than larvae. In addition the total number of larvae collected from M. pennsylvanicus was less than the number of nymphs from 1974 to 1977, (2706 larvae vs 4167 nymphs) (Table 2, Campbell and McKay 1979). The mammal trapping program employed by Campbell and McKay (1979) was biased to facilitate the capture of M. pennsylvanicus. This they accomplished by establishing a trapping grid of 20.12m intervals with additional traps located at 14m intervals diagonally between grid lines in field and ecotonal areas. As a result they trapped areas inhabited by M. pennsylvanicus and Peromyscus spp. at a greater rate than areas in the forest occupied by C. gapperi. In addition the total number of captures for M. pennsylvanicus was 1130, Peromyscus spp. 922, and C. gapperi 458,

indicates that C. gapperi may be under represented.

Differences in the reported distribution of larvae and nymphs in Nova Scotia and Birds Hill appear to be partially due to different trapping schedules employed as well as the failure by Campbell and McKay (1979) to differentiate Peromyscus leucopus from P. maniculatus.

Gkoroba (1980) found that C. gapperi and P. maniculatus were the two most important hosts of D. variabilis larvae and nymphs during his study conducted at Delta Marsh, Manitoba. He reported that these two species of myomorph rodents were found almost exclusively in forested areas. This observation implies that larvae and nymphs were most commonly encountered in the forest. Though the distribution of immature ticks at Delta Marsh appears to be similar to that found by the author at Birds Hill, there is a slight discrepancy over the observed behaviour of P. maniculatus.

At Birds Hill P. maniculatus was rarely collected from forested areas unlike Gkoroba's (1980) population which was almost exclusively boreal. Iverson and Turner (1973) identified the presence of three subspecies of Peromyscus in southern Manitoba with different habitat preferences. P. m. bairdii, the prairie deer mouse, occurs in disturbed grasslands, fields and brushy areas of southern and western Manitoba. P. m. maniculatus and P. m. gracilis are both forest dwelling subspecies, the first in northeastern Manitoba and the second in southeastern Manitoba extending into Minnesota (Iverson et al. 1967; Iverson and Turner 1973). Gkoroba (1980) was apparently working with a different subspecies of Peromyscus maniculatus at Delta Marsh than the one encountered at Birds Hill which was most likely P. m. bairdii.

The relationship of D. variabilis larvae and nymphs with vegetation types is highly variable, and it appears that tick distribution is less dependent on vegetation types than it is on the dominant myomorph rodent species in an area.

Much effort has gone into examining the distribution of D. variabilis life stages in relation to vegetation types and hosts though little has been said about the different distribution patterns exhibited by larval and nymphal populations. During this study, data on the spatial distribution of larvae and nymphs were analysed to describe differences in aggregation levels. As a result it was concluded that larvae are highly aggregated in various habitats and that aggregates occupied a very small area within a research plot. Nymphs were generally less aggregated than larvae and tended to occupy a greater area within favourable habitats. Nymphal aggregates appeared to be centred over areas where larvae were previously aggregated and extended outwards into areas where larvae had not been collected. The distribution pattern of nymphs appears to be the result of dispersal of individuals away from the centre of larval aggregates by host movements.

Dispersal of D. variabilis immatures

Dispersal within the context of this study refers to the phenomenon by which larvae and nymphs are moved from one point to another. The distribution of larvae and nymphs is the end product of both the dispersal and removal of individuals from a population. Individuals can be removed from a population at any time through death but dispersal appears to act discontinuously throughout an individual's lifespan.

D. variabilis is generally considered to be a poor self-directed disperser. Sonenshine et al. (1966) reported that "... adults molting from engorged nymphs apparently move only very short distances prior to attachment to adult hosts"¹, based on his finding that marked ticks on an average moved between 16.0 and 3.1 feet over an entire season. Larvae and nymphs are unlikely to move any further than adults since they are considerably smaller and more vulnerable to dessication.

During the course of this study, laboratory-reared larvae formed dense clusters when placed in an arena. Disrupted clusters reformed in a few hours, often over the same point. This observation suggested that an aggregation pheromone may be present, similar to that reported in adults (Layton and Sonenshine 1975). This type of behavioural adaptation would serve to prevent the dispersal of individuals prior to host contact. Frequency distributions of larvae and nymphs on hosts during this study were found to be over-dispersed fitting either negative binomial or polynomial distribution patterns. Campbell (1979) reported similar results and suggested that there are clumped masses of both larvae and nymphs distributed within an area which only a few hosts actually contact.

It appears that the dispersal of D. variabilis immatures is necessarily a host dependent phenomenon (Sonenshine 1973) restricted to that period of the tick's life in contact with a host. The distance that an individual tick is dispersed is dependent on the host's species, sex, age, physical condition and a number of complex factors affecting the host's population structure.

Two types of movement are recognized for individuals of small mammal

¹Sonenshine, D.E., E.L. Atwood and J.T. Lamb. 1966. The ecology of ticks transmitting Rocky Mountain spotted fever in a study area in Virginia. Ann. Entomol. Soc. Amer. 59:1234-1262.

populations, dispersal and migration. "Dispersal is defined as movements of only a short distance made by individuals away from a natal site".¹ Dispersal is a continuous process and occurs either within or between generations. Migration is defined by Gaines and McClenaghan (1980) to be long directional movements made by individuals or groups at specific time periods within a generation. In some species, groups may leave and return in mass. Migration as defined does not appear to apply to the small mammal populations involved in tick ecology studies.

During the course of this study, nymphs were regularly collected from sites some distance from sites which produced larvae, and nymph populations were generally found to have lower indices of aggregation while occupying a greater area. These three observations indicate that populations of larvae are dispersed by rodents to produce the observed distribution of nymphs.

The most important disperser of larvae and nymphs during this study was the red-backed vole, C. gapperi. The importance of M. pennsylvanicus, P. maniculatus and Z. hudsonius to the dispersal of larvae and nymphs appears to vary from year to year.

Examination of the small mammal literature reveals that not all species of rodents have the same dispersal capabilities. The size of individual home ranges is greater for males than females and social or colonial species have smaller home ranges than do the asocial species. M. pennsylvanicus and P. maniculatus are two colonial species according to Banfield (1977) for which he reports home ranges of .1 to .5 acres

¹From Gaines, M.S. and L.R. McClenaghan, Jr. 1980. Dispersal in small mammals. *Ann. Rev. Ecol. Syst.* 11:163-196.

and 1.4 to 2.4 acres respectively; upper limits for ranges are for males. C. gapperi, an aggressive asocial species is reported to have very large home territories. Males may occupy up to 3.5 acres (Banfield 1977).

Z. hudsonius is reported to be asocial, but tolerant of other individuals, with maximum home ranges for females and males being 2.0 and 3.2 acres respectively (Whitaker 1963).

Dispersal of individual rodents was observed directly and indirectly during this study. Release of individually tagged animals allowed direct measurement of dispersal distances subject to subsequent recapture. The distributions of captures for species were observed to change over time, indirectly demonstrating dispersal of individuals into previously unoccupied areas.

Direct measurements of dispersal distances were most reliable for species with high recapture rates, such as M. pennsylvanicus. P. maniculatus and Z. hudsonius. M. pennsylvanicus recaptures were most often from the site of release or less often from an adjacent site 20m away. Z. hudsonius recaptures rarely came from the same site as released or even from adjacent sites. Individuals were observed to travel as far as 80m between captures. P. maniculatus recaptures were commonly from a group of 2 to 4 adjacent sites covering an area of roughly 400-600m². C. gapperi recapture rates were generally very low and few individuals were captured more than twice.

Dramatic changes in population distribution patterns between years were noted for three species of myomorph rodents and one squirrel during this study. P. maniculatus invaded plot one in 1980 where it was absent the previous season. On plot two in 1980 the range of the P. maniculatus

population extended well into certain parts of the forest where it was not present in 1979. C. gapperi populations on plot two occupied over 90% of the trap sites within the forest in 1980 and extended beyond the ecotone into the field while in 1979 this species occupied less than 60% of the forest sites and only a few ecotone sites. Similar range extension was noted for C. gapperi on plot one in 1980. The M. pennsylvanicus population on plot one in 1980 had a substantially reduced range when compared to that occupied in 1979. The drastic restructuring of the small mammal community from year to year must inevitably effect the distribution and even the very survival of D. variabilis immatures.

Changes in the distributions of C. gapperi and P. maniculatus populations occurred at certain times during the summer months and were detected by the sampling program. During the second recruitment or reproductive cycle of C. gapperi in July of 1980, many individuals were captured for the first time in the ecotone and field areas of plot two, many of these individuals were infested with D. variabilis nymphs. Similar movements were observed on plot one in 1980 during the same period. In 1979 movement of C. gapperi into vacant areas of plot one occurred in late August during the same period as the third reproductive cycle. None of these individuals were found infested by nymphs. P. maniculatus populations were relatively small when compared to C. gapperi and the only evidence of population redistribution occurred on plot two in 1980, when increased numbers of individuals were captured in forested areas. The relationship between forest captures and reproductive cycles was not clear because of the small numbers involved.

Admittedly the results of this study do not clearly demonstrate that

dispersal of the three cricetid species of myomorph rodents, M. pennsylvanicus, C. gapperi and P. maniculatus, is related to their reproductive cycles. However several hypotheses have been proposed by mammalogists as mechanisms of rodent dispersal based on population densities (Gaines and McClenaghan 1980).

The social subordination hypothesis proposed by Christian (1970) states that as population density increases, competition is increased leading to elevated levels of aggression between individuals. Aggressive individuals drive social subordinates to disperse into suboptimal habitats. Dispersal within the context of this hypothesis, is a density dependent phenomenon.

The social subordination hypothesis results in the following predictions according to Gaines and McClenaghan (1980): a) levels of population density and aggression and will be positively correlated, b) dispersal rates will be higher during phases of peak density than during phases of increasing density, c) aggression and dispersal will be physiological responses to density, d) dispersers will be predominantly subadult males that are social subordinates.

The genetic-behavioural hypothesis by Chitty (1967) and Krebs (1978) assumes that spacing behaviour and dispersal regulates cycles in microtine rodents. Natural selection of genotypes favours individuals with high reproductive output in early phases of population growth and aggressive individuals exhibiting territorial spacing behaviour at high densities.

The basic difference between the social subordination hypothesis and the genetic-behavioural hypothesis is the cause of the increased

aggression in a population, physiological changes in the former and genetic selection in the latter. Both hypotheses have in common the prediction that populations with increasing density are more likely to demonstrate dispersal than those with decreasing density.

Gaines and McClenaghan (1980) summarized dispersal of territorial small mammals as being a function of increasing population density usually following periods of reproductive activity. In the case of the cricetid rodents there are at least three and possibly four reproductive cycles between spring and fall (Banfield 1977) every year. Z. hudsonius and the sciurids, S. franklinii, S. tridecemlineatus and T. striatus are reported to have only one annual reproductive cycle in Manitoba and central North America, (Banfield 1977; Smith and Smith 1972; Whitaker 1963; McCarley 1966; Rongstad 1965).

It appears then that greatest dispersal of D. variabilis larvae and nymphs is most likely to occur in association with a cricetid host species undergoing an increase in population density during reproductive cycles. Such a relationship between ticks and small mammals would insure that ticks have a maximum probability of contacting hosts while insuring dispersal into new habitats or areas being colonized by hosts. Subsequent sections of this discussion include an examination of this relationship and its implications.

Seasonal dynamics of D. variabilis immatures

The activity cycles for D. variabilis larvae and nymphs were each unimodal during this study. The peak of larval activity occurred between late May and early June each year preceding the nymphal activity peak

in mid-July by approximately four to five weeks. The onset and termination of the respective activity periods was variable from year to year suggesting that a small but variable proportion of the larval and nymphal populations initiate activity in response to stimuli not affecting the majority of the populations. Variable responses to stimuli may be due to intrinsic behavioural adaptations and/or to regional variations in the strength of stimuli.

Larvae and nymphs were most active at Delta Marsh, Manitoba in 1977 during the months of June and July respectively (Gkoroba 1980). In 1978, Gkoroba found that larval activity peaked between late May and early June while nymphal activity peaked in July. Furthermore, he also noted that the position of the nymphal activity period was constant between years and that seasonal activity of larvae and nymphs was unimodal.

Garvie et al. (1978) reported that larval activity was occasionally bimodal with one period "... occurring during May and June. Subsequently, larval activity declined to low levels in July and early August, but sometimes would increase again with a secondary midsummer peak in late August".¹ They also found that nymphal activity was unimodal occurring during June and July. Garvie et al. (1978) concluded that the majority of the D. variabilis population in Nova Scotia requires two years to complete its life cycle. Gkoroba (1980) reached similar conclusions about the life span of D. variabilis at Delta Marsh, influenced in part by the Garvie et al. (1978) study.

¹Garvie, M.B., et al. (1978) Seasonal dynamics of American dog tick, Dermacentor variabilis (Say), populations in Southwestern Nova Scotia. Can. J. Zool. 56:28-39.

The seasonal dynamics of D. variabilis populations at Birds Hill conformed with the results of both Gkoroba (1980) and Garvie et al. (1978). The Garvie et al. (1978) study was the only Canadian project to note occasional bimodal activity patterns for larvae. It therefore seems appropriate to attribute a two year life cycle to the populations of D. variabilis at Birds Hill, Manitoba.

D. variabilis adults and larvae were the main overwintering stages at Birds Hill, becoming active shortly after snowmelt. The peak of adult activity occurred between the middle of May and late June as in other Canadian studies (Garvie et al. 1978; Gkoroba 1980). Larvae born to the spring adult cohort are assumed to overwinter unfed before emerging the following spring to feed (Garvie et al. 1978; Sonenshine 1979). Nymphs are assumed to molt to adults in late summer and overwinter unfed (Garvie et al. 1978; Sonenshine 1979; McEnroe 1978b).

The distribution of D. variabilis life stages with respect to host species and vegetation types appeared highly variable during this study. The temporal distribution of the majority of larvae and nymphs was remarkably consistent during this study and in other studies (Garvie et al. 1978; Gkoroba 1980). Gkoroba (1980) stated that, "Synchronization of life history, vegetation, seasonal climate and host populations has clear advantages to the parasite".¹ Campbell (1979) alluded to the role of temporal synchronization of tick life stages with host species when he suggested that the variable distribution of ticks may be due in part to "... interspecific differences in the timing of seasonal activity and

¹Gkoroba, K.G. 1980. A study of the seasonal population dynamics of the ticks, Dermacentor variabilis (Say) and Haemaphysalis leporispalustris (Packard) in a marshland habitat. Unpubl. M.Sc. Thesis. Univ. of Manitoba. 203 pp.

density of the mammal hosts ..."¹

Temporal synchrony of D. variabilis immatures
with cricetid reproductive cycles

Any discussion of tick ecology invariably introduces numerous questions about the tick-host interactions from a spatial viewpoint but the temporal synchrony of tick life stages with various host activity patterns has been virtually ignored. The development of a successful host-parasite relationship depends on the spatial and temporal synchrony of the two components and finally on their compatibility.

The three species of cricetid rodents encountered during this study, C. gapperi, M. pennsylvanicus and P. maniculatus, are all polyoestrus and capable of three to four reproductive cycles annually (Banfield 1977). Z. hudsonius, a zaptodid species, is reported to have two reproductive cycles in warmer areas of eastern North America and one cycle in the northern areas (Whitaker 1963). The three species of sciurids, S. franklinii, S. tridecemlineatus and T. striatus, are reported to be monoestrus in western Canada (Banfield 1977; Smith and Smith 1972). The dominant hosts of D. variabilis larvae and nymphs have consistently been polyoestrus cricetid rodents in this study and those of Gkoroba (1980), Garvie et al. (1978), Sonenshine et al. (1966), Sonenshine (1975), Campbell (1979) and Stout (1978).

The timing of reproductive cycles of cricetid rodents has been well documented in field and laboratory studies and some interesting

¹Campbell, A. (1979) Ecology of the American dog tick, Dermacentor variabilis, in southwestern Nova Scotia. In: Recent Advances in Acarology. 1978. ed. J.G. Rodriguez. Academic Press, page 140.

similarities and differences are apparent. P. maniculatus may have several litters in a season but peaks of reproduction occur in the spring and fall with a lull during the summer (Banfield 1977). This lull overlaps the period of peak nymphal activity, July, in Manitoba. P. leucopus an eastern species, however is reported to have peaks of litter production in April, then late June or early July followed by a lull into late August after which two more litters may be produced. As a result the second litter peak occurs during the peak of nymphal activity reported by Garvie et al. (1978) and Sonenshine (1979). Both species of Peromyscus have peaks of litter production just prior to or during the period of maximum larval activity, late May to early June.

C. gapperi is reported to have three peaks of litter production between April and October, the first in May, second in July and third in September (Banfield 1977). During this study three periods of maximum recruitment marked by an increased proportion of juveniles were noted seasonally for C. gapperi, in May, July and late August or September.

The reproductive effort of M. pennsylvanicus is apparently continuous. Females are capable of producing a litter every three weeks once they are 25 days old. However Banfield (1977) indicated that an average of 3.5 litters during a season is typical under field conditions.

During the course of this study recruitment or reproductive periods were most clearly seen in the C. gapperi populations and less so for the other cricetids. Trapping success and population density strongly influence the sensitivity with which changes in the rodent population density and structure may be detected. The following discussion will

deal primarily with the relationship between C. gapperi and D. variabilis immatures.

The larval activity period coincided with the first reproductive cycle of C. gapperi populations every year at Birds Hill. Over 90% of all larvae collected from this host came from individuals captured during this period only. Less than 20% of the individuals captured during any reproductive cycle were recaptured during a subsequent cycle.

The second recruitment cycle coincided with the nymphal peak of activity in July so closely that at first it was thought simply to be an artifact of increased captures. However upon closer examination this was discounted since both the prevalence and intensity of infestations increased at the peak of nymphal activity indicating that the trend was independent of the number of hosts examined. Individuals of the second reproductive cycle were the most important dispersers in 1980. Over 90% of all nymphs collected from this species were attributed to members of the second reproductive period. By the end of July or the beginning of August nymphal activity virtually ceased.

Individual voles attributed to the third reproductive cycle in late August were rarely infested by either nymphs or larvae.

The synchronization of D. variabilis larvae and nymphs with the first and second reproductive cycles of C. gapperi is accomplished in an unknown manner. Sonenshine (1979) has suggested that sustained larval activity in northern areas of the D. variabilis range is delayed until mid-May with the seasonal peak in late May or early June, and that the peak of nymphal activity is correspondingly delayed until early July. In addition adult activity has been modified so that teneral adults

developed late in the summer are inhibited from feeding until the subsequent spring so that only one cohort of adults feeds annually. Atwood and Sonenshine (1967) reported that sustained larval activity occurred when average daily solar radiation at ground level exceeded 200 langley's/day, and solar radiation apparently also influenced adult questing behaviour in spring. McEnroe and McEnroe (1973) and McEnroe (1975; 1978a) reported that the initiation of adult questing behaviour in the spring was dependent on soil temperatures and humidity. However no studies have uncovered the mechanisms for the suppression of larval and adult activity in late summer, though some authors have suggested possible reasons for this behavioural adaptation.

McEnroe (1978b) suggested that both summer larval and adult attachment is limited by the development of resistance in host populations following previous exposure in the spring. This theory is based on the work of Trager (1939) who found that deer mice and guinea pigs could develop resistance to tick feeding in as little as 2 weeks from the start of the first infection. Several other researchers have recently demonstrated immunological resistance to ticks by lab animals (Allen 1973; Boese 1974; Wikel 1979; Wikel et al. 1978).

Brown (1977) found that D. variabilis nymphs reared on guinea pigs exposed to nymphs 21 days earlier, experienced, a) prolonged feeding, b) reduced feeding success, c) increased molting times, and d) increased mortality during molting. In light of this evidence McEnroe's (1978b) suggestion, that summer hatched larvae are inhibited from feeding in the same season to avoid host resistance, has a great deal of merit. How then does delayed initiation of larval and nymphal feeding serve to

reduce the probability of ticks encountering immune hosts?

Trager (1939) reported that immunity to ticks by guinea pigs lasted at least three months. Banfield (1977) reported that the average life span of M. pennsylvanicus under field conditions was less than four weeks during the summer months. In general the lifespans of cricetids under field conditions are quite short and cricetid populations more or less represent semi-annual crops. It appears that if ticks delay their activity sufficiently, then a) host immunity may regress sufficiently to allow successful feeding or, b) the immune hosts will simply die out, to be replaced by their non-immune offspring. The results of this study indicated that very few C. gapperi or M. pennsylvanicus survived from one reproductive period to the next and none of the summer population survived through to the following spring, indicating the possibility of a fourth reproductive cycle in September or October. Higher rates of overwinter survival were observed for the sciurids, Z. hudsonius and P. maniculatus. D. variabilis appears to have solved the problem of encountering immune hosts by directing its life strategy to the short lived prolific cricetid species.

The temporal segregation of D. variabilis larvae and nymphs to distinct periods of time coincident with different generations of cricetids not previously exposed to ticks satisfies the requirement that each stage avoid contact with potentially immune hosts. The alternative of host selection by ticks would be impractical since the majority of hosts are territorial. If a larva or nymph encounters an immune host and detaches it is unlikely to contact another host within the same territory during the primary occupant's life time.

The temporal synchrony of D. variabilis life stages with host seasonal dynamics is an important aspect of its ecology and is accomplished by maintaining a fixed sequence and period for each life stage.

CONCLUSIONS

- 1) The majority of D. variabilis populations undergo a two-year life cycle in Manitoba.
- 2) The most important hosts of D. variabilis larvae and nymphs are the polyoestrus cricetid species, which include C. gapperi, M. pennsylvanicus and P. maniculatus.
- 3) The distribution and abundance of tick life stages with respect to different habitats (or vegetation types) are due to:
 - a) differential mortality in various microhabitats,
 - b) the availability of compatible hosts in an area,
 - c) the habitat preference of the dominant host species,
 - d) the dispersal movements of the host species, and not to tick vegetation preferences.
- 4) Dispersal of larvae and nymphs away from the natal site is a function of host dispersal which is greatest following periods of host reproductive activity.
- 5) The activity peaks of the D. variabilis life stages occur at fixed time periods and in a specific sequence.
- 6) The periods of larval and nymphal activity coincide with the first and second annual reproductive cycles of cricetids respectively.
- 7) The temporal segregation of larval and nymphal stages to distinct periods of time coincident with different generations of hosts is proposed as an adaptation to avoid contact with potentially immune hosts while insuring a high probability of contacting non-immune hosts.

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*Original article not seen.

Table 1. Summary of mammal species captured for 1979-1980 on plots one and two, and the number of captures, individuals and recapture rates for each species.

Mammal species	Plot one						Plot two					
	1979			1980			1979			1980		
	Capt. ^a	Ind. ^b	R. R. ^c	Capt.	Ind.	R. R.	Capt.	Ind.	R. R.	Capt.	Ind.	R. R.
<u>Clethrionomys gapperi</u> (Vigors)	8	8	1.0	44	32	1.4	44	28	1.6	126	78	1.6
<u>Lepus americanus</u> Erxleben	1	1	1.0	0	0	-	1	1	1.0	2	2	1.0
<u>Microtus pennsylvanicus</u> (Ord)	32	22	1.5	4	4	1.0	20	11	1.8	24	16	1.5
<u>Mus musculus</u> Linnaeus	0	0	-	0	0	-	1	1	1.0	0	0	-
<u>Peromyscus maniculatus</u> (Wagner)	0	0	-	6	4	1.5	20	9	2.2	35	18	1.9
<u>Sorex cinerius</u> Kerr	0	0	-	0	0	-	0	0	-	7	7	1.0
<u>Spermophilus franklini</u> (Sabine)	91	28	3.3	50	30	1.7	30	16	1.9	27	16	1.7
<u>Spermophilus tridecemlineatus</u> (Mitchell)	61	21	2.9	3	3	1.0	5	3	1.7	0	0	-
<u>Tamias striatus</u> (Linnaeus)	8	4	2.0	0	0	-	7	6	1.2	11	7	1.6
<u>Tamiasciurus hudsonicus</u> (Erxleben)	0	0	-	0	0	-	4	4	1.0	2	2	1.0
<u>Zapus hudsonius</u> (Zimmerman)	28	21	1.3	15	9	1.7	8	6	1.3	14	9	1.6
TOTALS	229	105		122	82		140	85		248	155	
Trapping effort in days		26			28			17			28	

^aCapt. = captures.

^bInd. = individuals.

^cR.R. = recapture rate = capt./ind.

Table 2. The distribution of small mammal populations with respect to habitat types at Birds Hill, Manitoba and the proportion of each habitat utilized by various species, 1979-1980.

Species		Plot one						Plot two					
		Forest		Ecotone		Field		Forest		Ecotone		Field	
		1979	1980	1979	1980	1979	1980	1979	1980	1979	1980	1979	1980
<u>C. gapperi</u>	A	75	57	25	36	-	6.8	91	95	9	2	-	2
	B	21	79	9	27	-	23	59	96	11	30	-	23
<u>P. maniculatus</u>	A	-	17	-	83	-	-	35	48	35	40	30	11
	B	-	7	-	18	-	-	22	29	55	66	15	23
<u>M. pennsylvanicus</u>	A	6	-	68	25	25	75	-	-	25	16	75	83
	B	7	-	50	5	15	7	-	-	44	22	53	38
<u>Z. hudsonius</u>	A	25	33	67	60	7	7	36	61	50	38	13	-
	B	35	28	59	31	15	8	11	30	11	55	8	-
<u>S. franklinii</u>	A	58	43	42	57	-	-	86	63	14	33	-	4
	B	85	64	73	45	-	-	48	48	44	67	-	8
<u>S. tridecemlineatus</u>	A	18	33	45	66	37	-	-	-	20	-	80	-
	B	50	7	64	9	76	-	-	-	11	-	30	-
<u>T. striatus</u>	A	87	-	13	-	-	-	86	100	14	-	-	-
	B	50	-	5	-	-	-	22	26	11	-	-	-

A = % of captures (total for species) from each habitat.

B = % of traps in habitat occupied at least once during season.

Table 3. Host species' contribution to the total number of larvae collected on plots one and two, 1979-1980.

Host species	1979						1980					
	Plot one		Plot two		Pooled		Plot one		Plot two		Pooled	
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
<u>C. gapperi</u>	-	-	43	91	43	43	30	71	22	50	52	61
<u>P. maniculatus</u>	-	-	3	6	3	3	3	7	15	34	18	21
<u>M. pennsylvanicus</u>	48	89	1	2	48	47	8	19	-	-	8	9
<u>Z. hudsonius</u>	6	11	1	2	7	7	1	3	6	14	7	8
<u>S. franklinii</u>	-	-	-	-	-	-	-	-	1	2	1	1
<u>S. tridecemlineatus</u>	-	-	-	-	-	-	-	-	-	-	-	-
<u>T. striatus</u>	-	-	-	-	-	-	-	-	-	-	-	-
Total larvae	54		48		102		42		44		86	

Table 4. 1979-1980 larval infestation parameters of prevalence and intensity for small mammals by month on plots one and two.

Species	1979										1980									
	Plot one					Plot two					Plot one					Plot two				
	May	Jun	Jul	Aug	Sep	May	Jun	Jul	Aug	Sep	Apr	May	Jun	Jul	Aug	Apr	May	Jun	Jul	Aug
<u>C. gapperi</u>																				
Total captures	0	0	0	1	7	2	14	11	13	4	2	3	5	19	15	0	20	20	47	39
Infested captures	-	-	-	-	-	-	4	3	-	-	-	2	3	4	-	-	5	7	1	-
Prevalence (%)	-	-	-	-	-	-	29	27	-	-	-	66	60	21	-	-	25	35	2.1	-
Total larvae	-	-	-	-	-	-	37	6	-	-	-	14	11	5	-	-	8	13	1	-
Intensity	-	-	-	-	-	-	9.3	2.0	-	-	-	7.0	3.7	1.3	-	-	1.6	1.8	1.0	-
<u>M. pennsylvanicus</u>																				
Total captures	10	8	4	8	2	6	7	5	2	0	0	0	2	0	2	0	6	11	5	2
Infested captures	-	4	-	-	-	-	1	-	-	-	-	-	1	-	2	-	-	-	-	-
Prevalence (%)	-	50	-	-	-	-	14	-	-	-	-	-	50	-	-	-	-	-	-	-
Total larvae	-	47	-	-	-	-	1	-	-	-	-	-	8	-	-	-	-	-	-	-
Intensity	-	11.7	-	-	-	-	1.0	-	-	-	-	-	8.0	-	-	-	-	-	-	-
<u>P. maniculatus</u>																				
Total captures	0	0	0	0	0	1	4	8	6	1	0	0	1	3	2	0	2	10	11	12
Infested captures	-	-	-	-	-	-	2	-	-	-	-	-	1	-	-	-	1	3	1	-
Prevalence (%)	-	-	-	-	-	-	50	-	-	-	-	-	100	-	-	-	50	30	9	-
Total larvae	-	-	-	-	-	-	3	-	-	-	-	-	3	-	-	-	1	10	4	-
Intensity	-	-	-	-	-	-	1.5	-	-	-	-	-	3.0	-	-	-	1.0	3.3	4.0	-
<u>Z. hudsonius</u>																				
Total captures	3	20	1	3	1	0	3	2	2	1	0	2	10	3	0	0	7	5	2	0
Infested captures	0	2	0	0	0	-	1	0	0	0	-	0	1	0	-	-	3	0	0	-
Prevalence (%)	-	10	-	-	-	-	33	-	-	0	-	-	10	-	-	-	43	-	-	-
Total larvae	-	6	-	-	-	-	1	-	-	-	-	-	1	-	-	-	6	-	-	-
Intensity	-	3.0	-	-	-	-	1.0	-	-	-	-	-	1.0	-	-	-	2.0	-	-	-

Table 5. Host species' contribution to the total number of nymphs collected on plots one and two, 1979-1980.

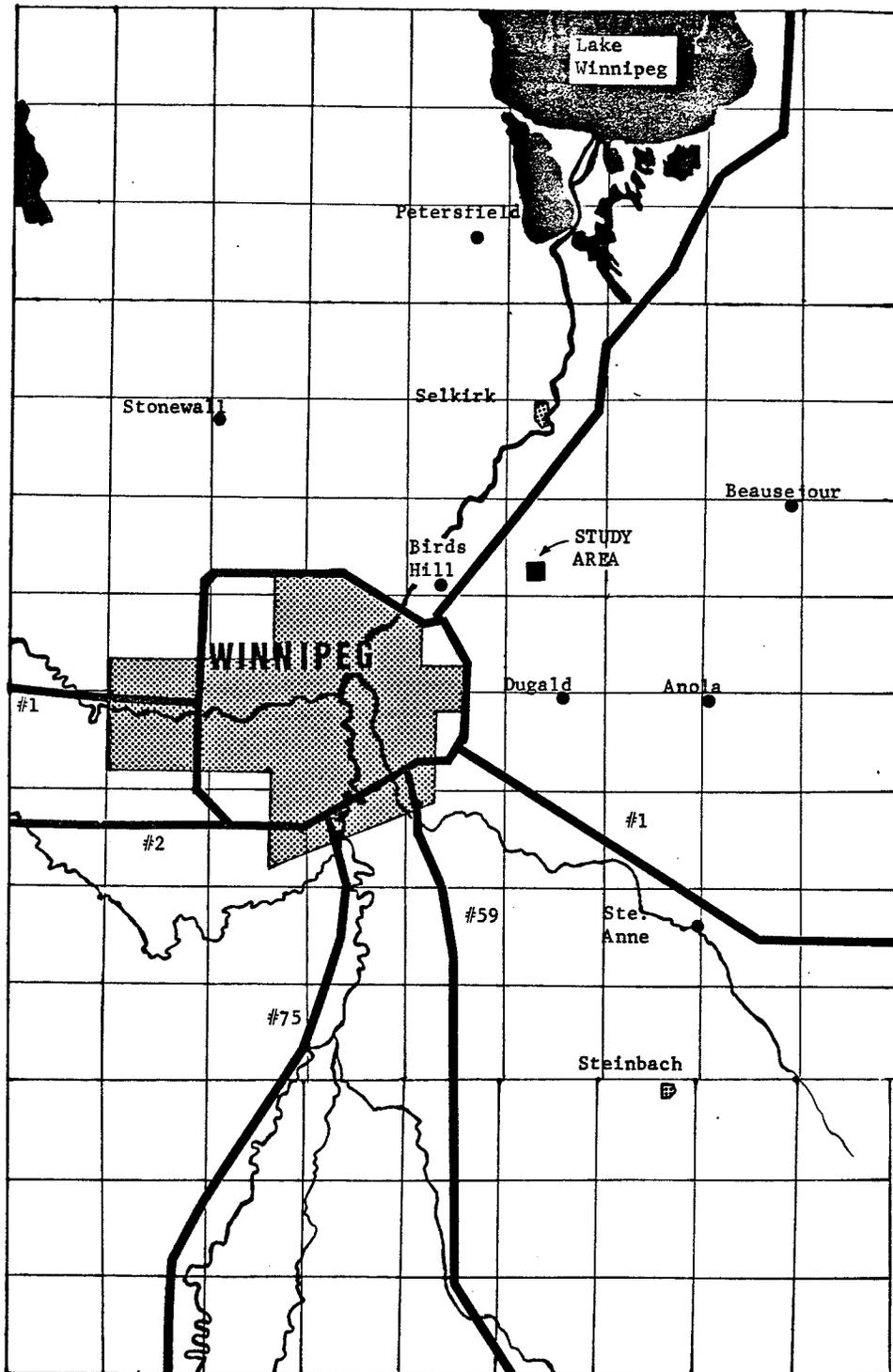
Host species	1979						1980					
	Plot one		Plot two		Pooled		Plot one		Plot two		Pooled	
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
<u>C. gapperi</u>	-	-	46	94	46	86	63	86	92	84	155	85
<u>P. maniculatus</u>	-	-	2	4	2	4	5	7	15	14	20	11
<u>M. pennsylvanicus</u>	2	50	-	-	2	4	-	-	-	-	-	-
<u>Z. hudsonius</u>	1	25	-	-	1	2	5	7	-	-	5	3
<u>S. franklinii</u>	-	-	-	-	-	-	-	-	-	-	-	-
<u>S. tridecemlineatus</u>	1	25	-	-	1	2	-	-	-	-	-	-
<u>T. striatus</u>	-	-	1	2	1	2	-	-	2	2	2	1
Total nymphs	4		49		53		73		109		182	

Table 6. 1979-1980 nymphal infestation parameters of prevalence and intensity for small mammals by month on plots one and two.

Species	1979										1980									
	Plot one					Plot two					Plot one					Plot two				
	May	Jun	Jul*	Aug	Sep	May	Jun	Jul	Aug	Sep	Apr	May	Jun	Jul	Aug	Apr	May	Jun	Jul	Aug
<u>C. gapperi</u>																				
Total captures	0	0	0	1	7	2	14	11	13	4	2	3	5	19	15	0	20	20	47	39
Infested captures	-	-	-	0	0	0	0	7	5	0	0	0	4	12	0	-	2	11	26	1
Prevalence (%)	-	-	-	-	-	-	-	63	38	-	-	-	80	63	0	-	10	55	55	3
Total nymphs	-	-	-	-	-	-	-	40	6	-	-	-	29	34	0	-	2	27	62	1
Intensity	-	-	-	-	-	-	-	5.7	1.2	-	-	-	7	2.8	0	-	1.0	2.5	2.4	1.0
<u>M. pennsylvanicus</u>																				
Total captures	10	8	4	8	2	6	7	5	2	0	0	0	2	0	2	0	6	11	5	2
Infested captures	0	1	0	0	0	0	0	0	0	-	-	-	0	-	0	-	0	0	0	0
Prevalence (%)	-	12.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Total nymphs	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Intensity	-	2.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<u>P. maniculatus</u>																				
Total captures	0	0	0	0	0	1	4	8	6	1	0	0	1	3	2	0	2	10	11	12
Infested captures	-	-	-	-	-	0	0	2	0	0	-	-	1	2	0	-	0	2	6	0
Prevalence (%)	-	-	-	-	-	-	-	25	-	-	-	-	100	66	-	-	-	20	55	-
Total nymphs	-	-	-	-	-	-	-	2	-	-	-	-	1	4	-	-	-	3	12	-
Intensity	-	-	-	-	-	-	-	1.0	-	-	-	-	1.0	2.0	-	-	-	1.5	2.0	-
<u>Z. hudsonius</u>																				
Total captures	3	20	1	3	1	0	3	2	2	1	0	2	10	3	0	0	7	5	2	0
Infested captures	0	1	0	0	0	-	0	0	0	0	-	0	1	1	-	-	0	0	0	0
Prevalence (%)	-	5.	-	-	-	-	-	-	-	-	-	-	10	33	-	-	-	-	-	-
Total nymphs	-	1	-	-	-	-	-	-	-	-	-	-	4	1	-	-	-	-	-	-
Intensity	-	1.0	-	-	-	-	-	-	-	-	-	-	4.0	1.0	-	-	-	-	-	-
<u>T. striatus</u>																				
Total captures	1	3	1	2	1	1	0	2	2	2	0	0	0	0	0	0	2	1	5	3
Infested captures	0	0	0	0	0	0	-	1	0	0	-	-	-	-	-	-	0	0	2	0
Prevalence (%)	-	-	-	-	-	-	-	50	-	-	-	-	-	-	-	-	-	-	40	-
Total nymphs	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	2	-
Intensity	-	-	-	-	-	-	-	1.0	-	-	-	-	-	-	-	-	-	-	1.0	-

* Note: One nymph collected from S. tridecemlineatus on plot one in Jul 1979.

Figure 1. Location of Birds Hill Park study area.



GRID= 9.6 km x 9.6 km (6 miles x 6 miles)

Figure 2. Aerial photograph of study area, showing the orientation of study plots.

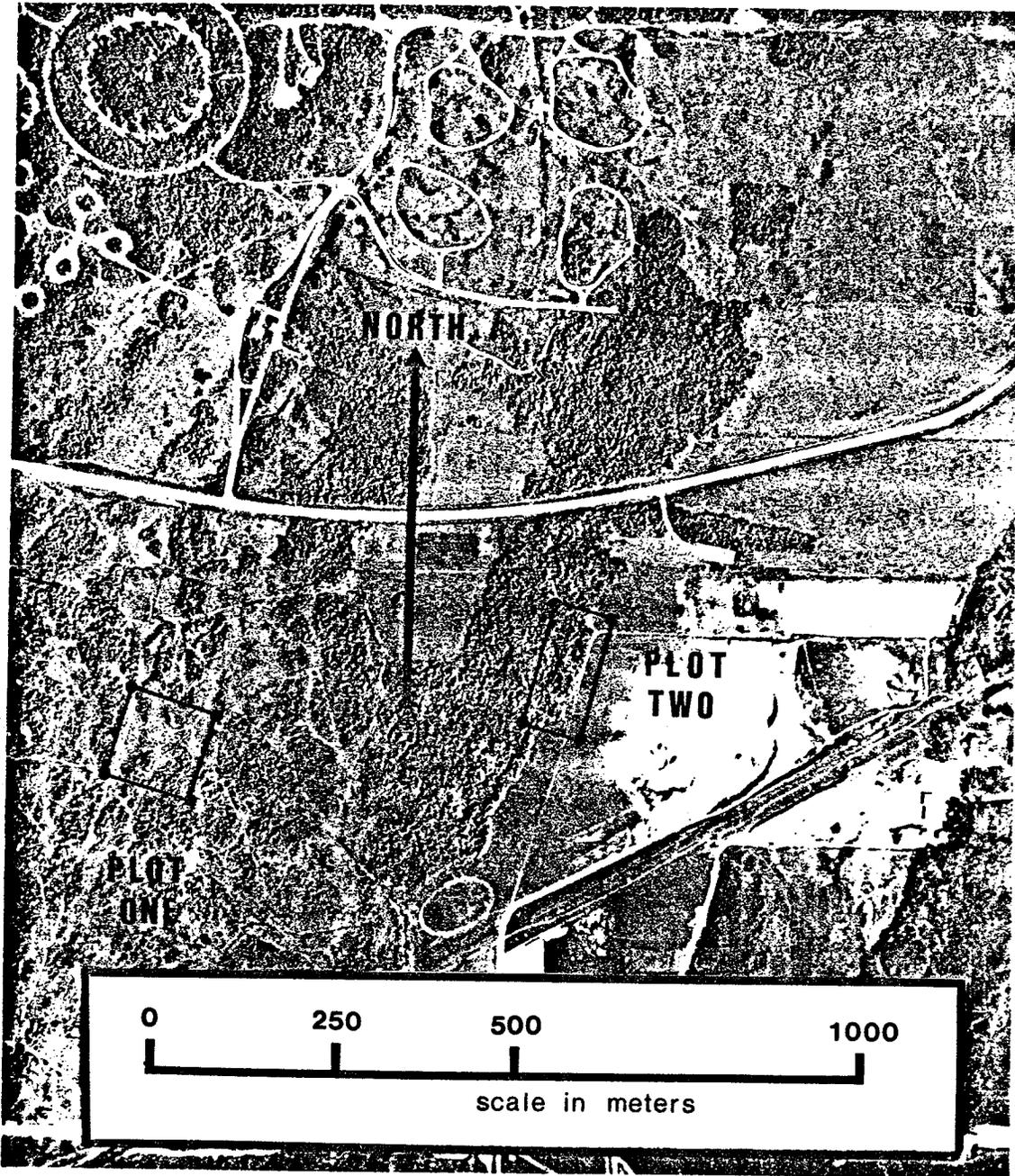


Figure 3. Tomahawk live trap model number 101 used to capture small rodents with shelter roof to protect trap from sun and rain.



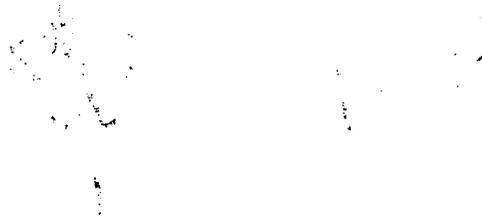


Figure 4. Number sequence assigned to toes of small mammals. By clipping a combination of toes a unique identification number (tag) could be assigned to each animal.

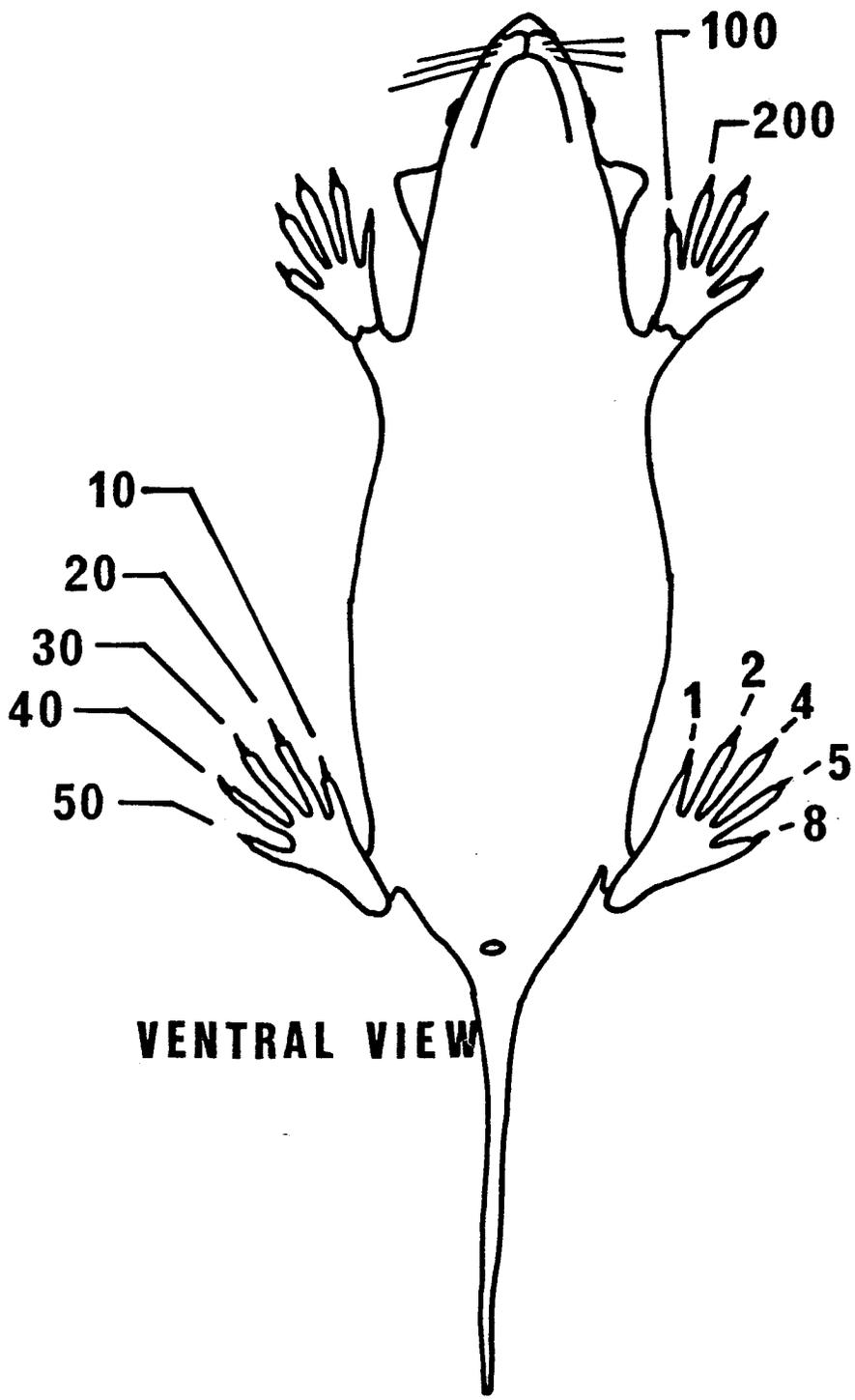
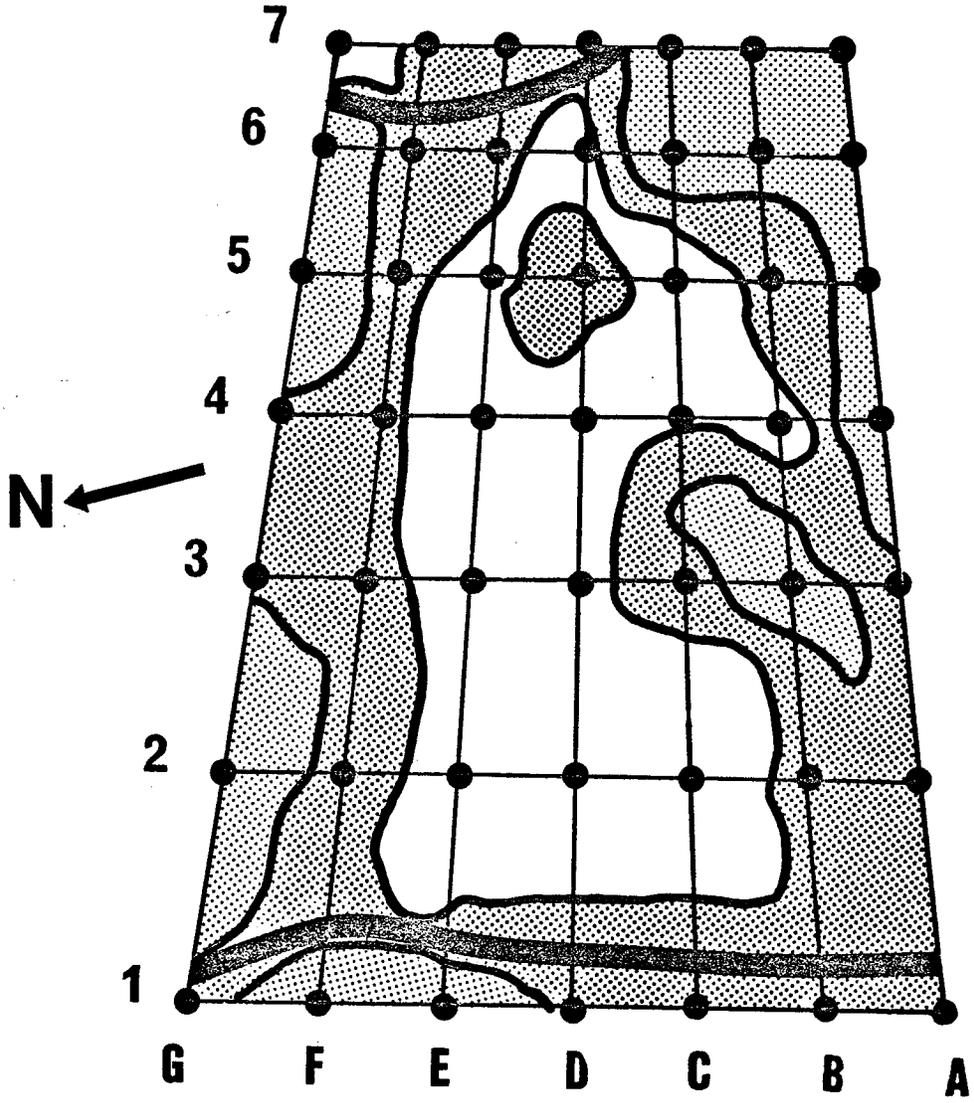




Figure 5. Study plot one showing trap grid layout and boundaries of the three habitats, forest, field and ecotone. (Persepctive view).



□ FIELD ▨ ECOTONE ▩ FOREST
 ● TRAPSITE — TRAIL

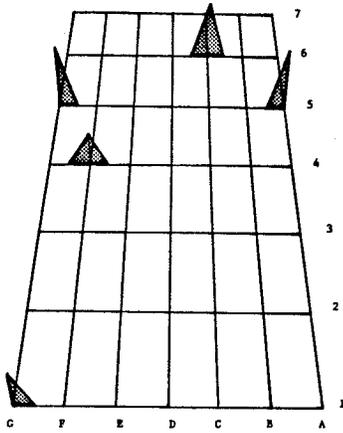
Figure 6. Perspective views of study plot one showing the distribution and frequency of rodent captures in relation to trap sites for species,

- a) Clethrionomys gapperi (Vigors) in 1979
- b) Microtus pennsylvanicus (Ord) in 1979
- c) Zapus hudsonius (Zimmerman) in 1979
- d) Spermophilus franklinii (Sabine) in 1979

A

CAPTURES PER TRAP SITE:

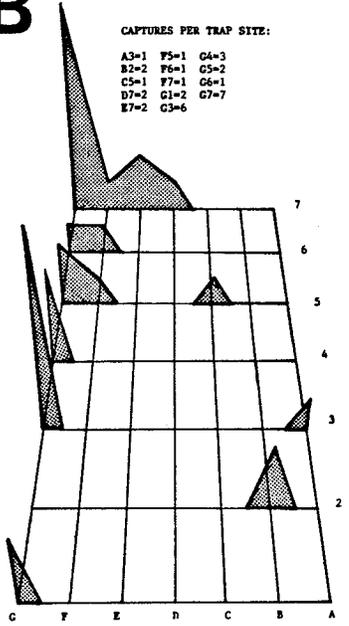
A5=2 G1=1
C6=2 G5=2
F4=1



B

CAPTURES PER TRAP SITE:

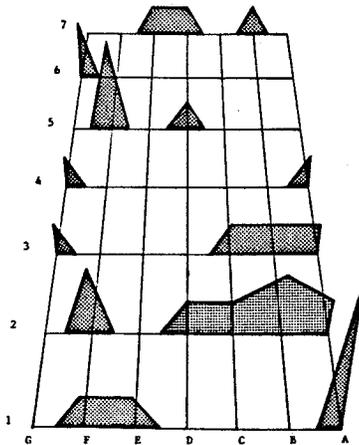
A3=1 F5=1 G4=3
B2=2 F6=1 G5=2
C5=1 F7=1 G6=1
D7=2 G1=2 G7=7
E7=2 G3=6



C

CAPTURES PER TRAP SITE:

A1=4 B3=1 D5=1 F2=2
A2=1 B7=1 D7=1 F5=3
A3=1 C2=1 E1=1 G3=1
A4=1 C3=1 E7=1 G4=1
B2=2 D2=1 F1=1 G6=2



D

CAPTURES PER TRAP SITE:

A1=6 B3=1 D1=7 F6=2
A2=1 B5=1 D5=1 G1=3
A5=7 B6=4 E1=3 G2=4
A6=2 B7=6 E7=1 G3=2
A7=8 C1=1 F1=5 G4=1
B1=3 C6=3 F2=2 G5=2
B2=1 C7=8 F5=1 G6=3

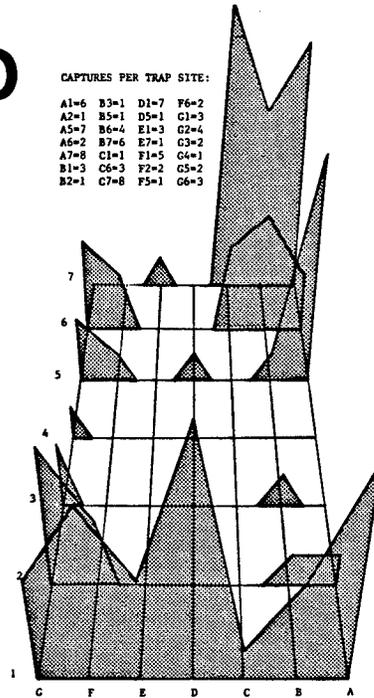


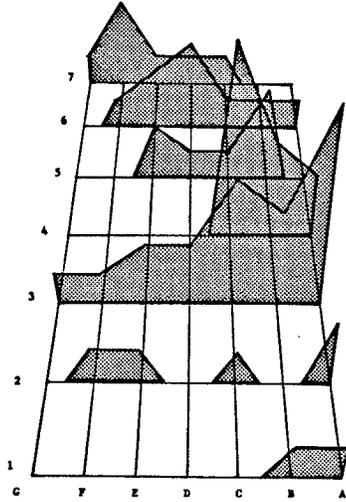
Figure 7. Perspective views of study plot one showing the distribution and frequency of rodent captures in relation to trap sites for species,

- a) Spermophilus tridecemlineatus (Mitchell) in 1979
- b) Spermophilus tridecemlineatus (Mitchell) and Microtus pennsylvanicus (Ord) in 1980
- c) Clethrionomys gapperi (Vigors) in 1980
- d) Peromyscus maniculatus (Wagner) in 1980

A

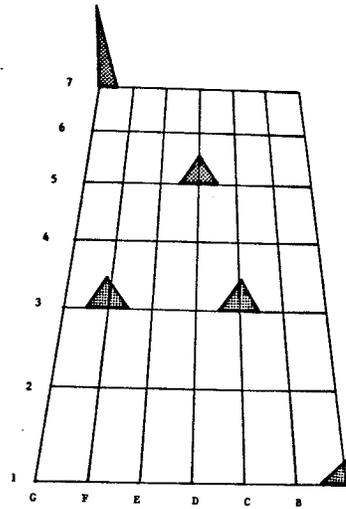
CAPTURES PER TRAP SITE:

A1=1 E3=3 C4=4 D6=3 E7=1 G7=1
 A2=2 E4=3 C5=1 D7=1 F2=1
 A3=6 E5=3 C6=1 E2=1 F3=1
 A4=2 E6=1 C7=1 E3=2 F6=1
 A5=1 C2=1 D3=2 E5=2 F7=3
 B1=1 C3=6 D5=1 E6=2 G3=1

**B**

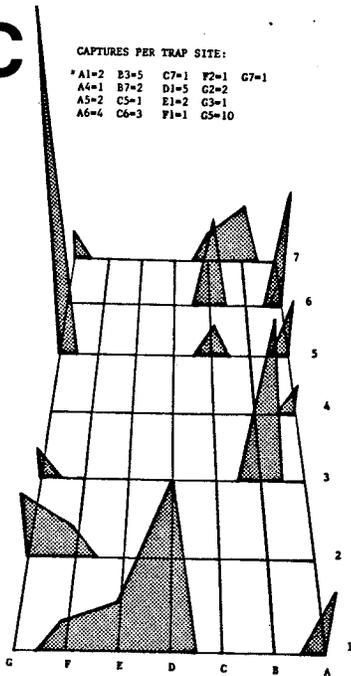
Captures per trap site for,
M. pennsylvanicus,
 D5=1 G7=3;

S. tridecimlineatus,
 A1=1 C3=1 F3=1

**C**

CAPTURES PER TRAP SITE:

A1=2 E3=5 C7=1 F2=1 G7=1
 A4=1 B7=2 D1=5 C2=2
 A5=2 C5=1 E1=2 G3=1
 A6=4 C6=3 F1=1 G5=10

**D**

Captures per trap site:

A1=2 F1=1
 B1=1 G1=1
 G1=1

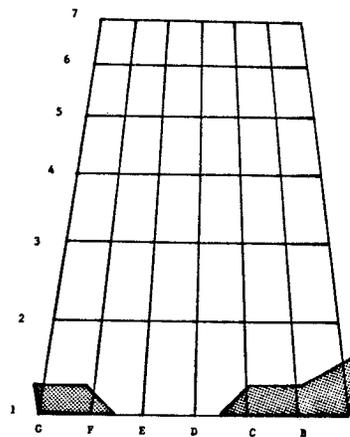
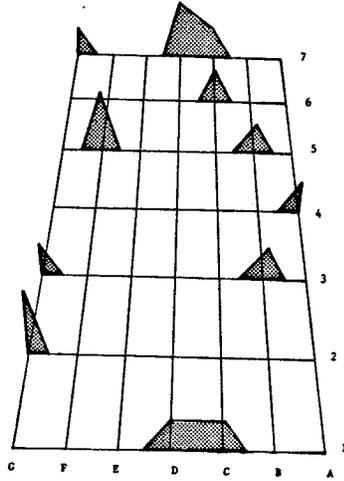


Figure 8. Perspective views of study plot one showing the distribution and frequency of rodent captures in relation to trap sites for the species,

- a) Zapus hudsonius (Zimmerman) in 1980
- b) Spermophilus franklinii (Sabine) in 1980

A

Captures per trap site:
A4=1 C1=1 D1=1 G2=2
B3=1 G6=1 D7=2 G3=1
B5=1 C7=1 F5=2 G7=1



B

Captures per trap site:
A1=3 B5=1 C7=6 F1=1
A2=1 B6=5 D1=6 G2=1
A3=2 B7=2 D7=2 G3=1
A5=3 C1=3 E1=7 G6=1
A7=1 G6=2 E7=4

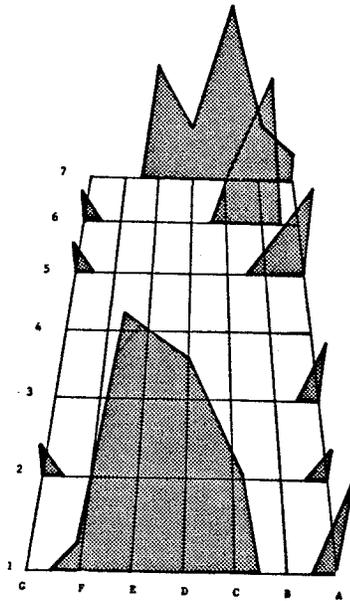
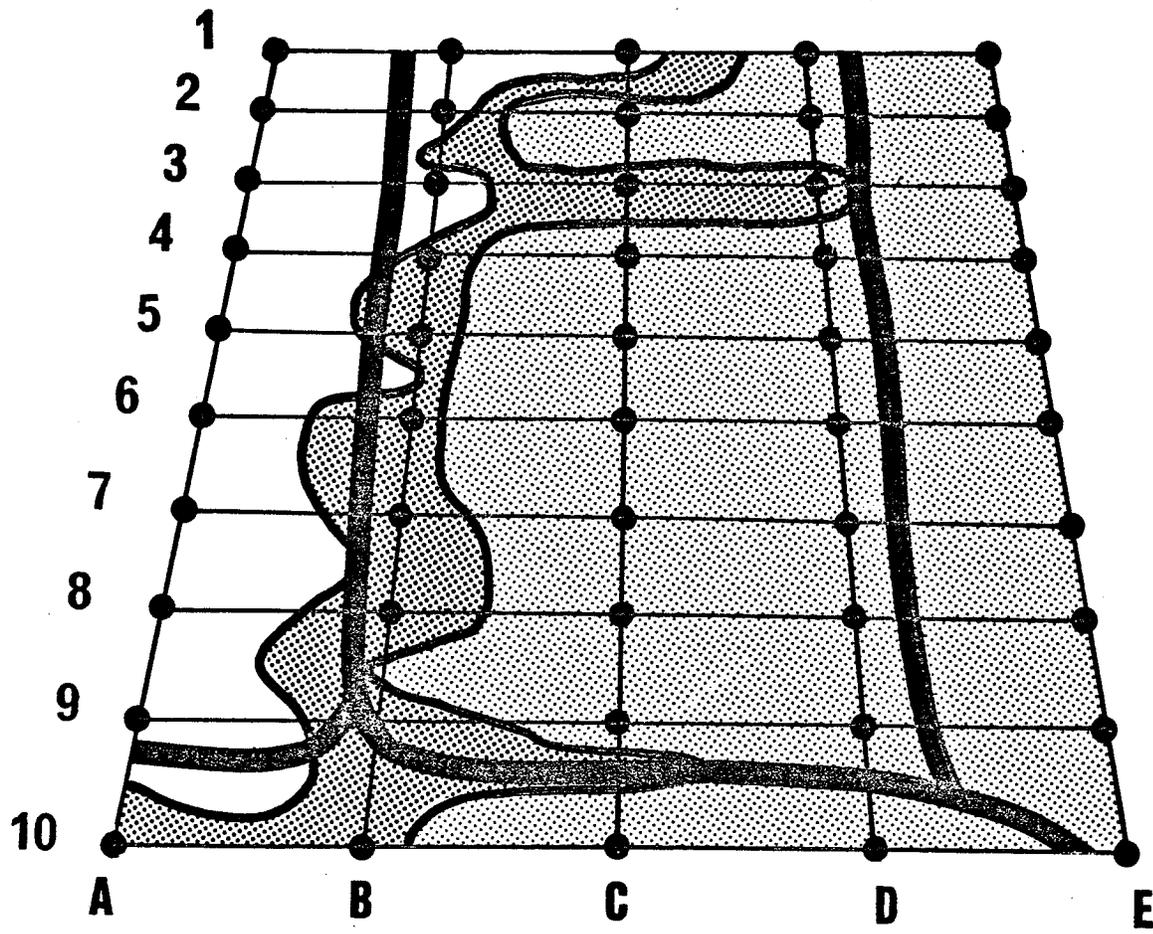


Figure 9. Study plot two showing trap grid layout and boundaries of the three habitats; forest, field and ecotone. (Perspective view).



□ FIELD ▨ ECOTONE ▩ FOREST
● TRAPSITE ——— TRAIL

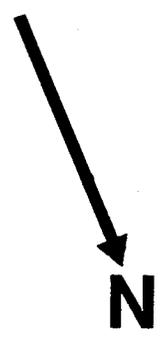


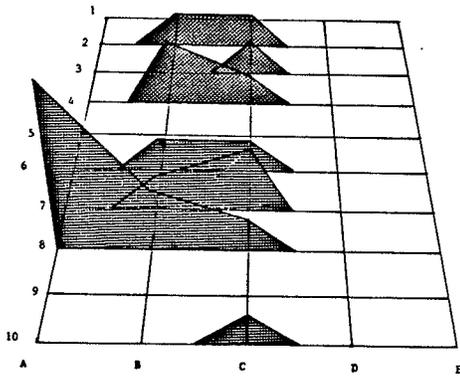
Figure 10. Perspective views of study plot two showing the distribution and frequency of rodent captures in relation to trap sites for the species,

- a) Peromyscus maniculatus (Wagner) in 1979
- b) Clethrionomys gapperi (Vigors) in 1979
- c) Microtus pennsylvanicus (Ord) in 1979
- d) Zapus hudsonius (Zimmerman) in 1979

A

Captures per trap site:

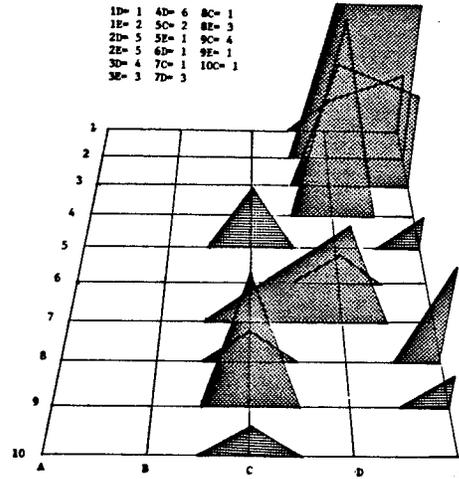
2B= 1	6B= 1	8B= 2
2C= 1	6C= 1	8C= 1
3C= 1	7B= 1	10C= 1
4B= 2	7C= 2	
4C= 1	8A= 5	



B

Captures per trap site:

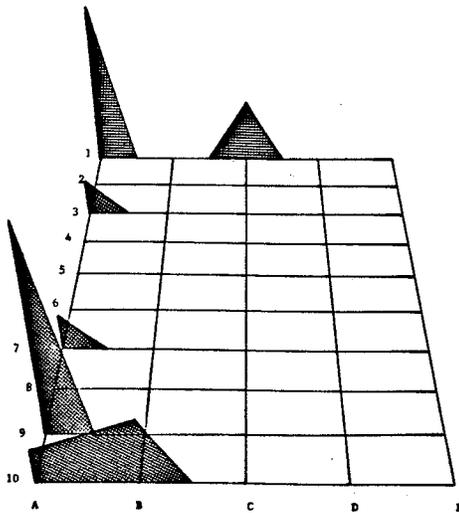
1D= 1	4D= 6	8C= 1
1E= 2	5C= 2	8E= 3
2D= 5	5E= 1	9C= 4
2E= 5	6D= 1	9E= 1
3D= 4	7C= 1	10C= 1
3E= 3	7D= 3	



C

Captures per trap site:

1A= 5	9A= 6
1C= 2	10A= 1
3A= 1	10B= 2
7A= 1	



D

Captures per trap site:

4E= 1	8C= 1
7A= 1	10A= 4
7E= 1	

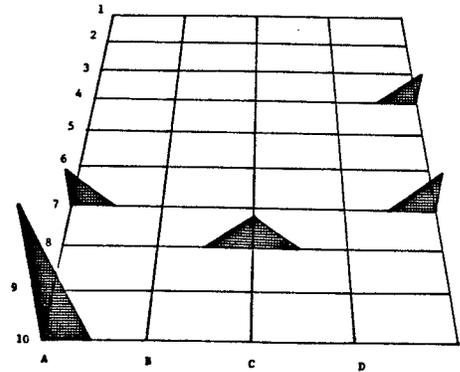


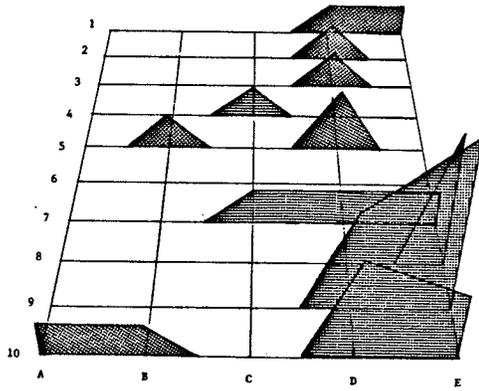
Figure 11. Perspective views of study plot two showing the distribution and frequency of rodent captures in relation to trap sites for the species,

- a) Spermophilus franklinii (Sabine) in 1979
- b) Peromyscus maniculatus (Wagner) in 1980
- c) Clethrionomys gapperi (Vigors) in 1980
- d) Microtus pennsylvanicus (Ord) in 1980

A

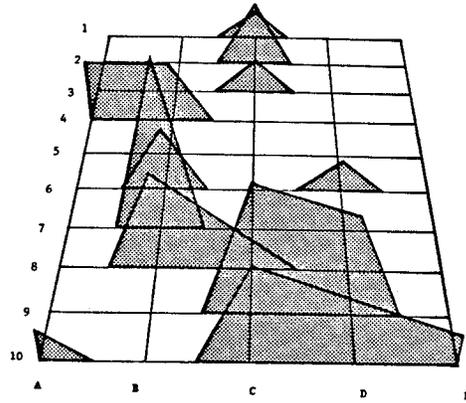
Captures per trap site:

1D= 1 5D= 2 9E= 5
 3E= 1 7C= 1 10A= 1
 2D= 1 7B= 1 10B= 1
 3D= 1 7E= 1 10D= 3
 4C= 1 8E= 4 10E= 2
 5B= 1 9D= 3

**B**

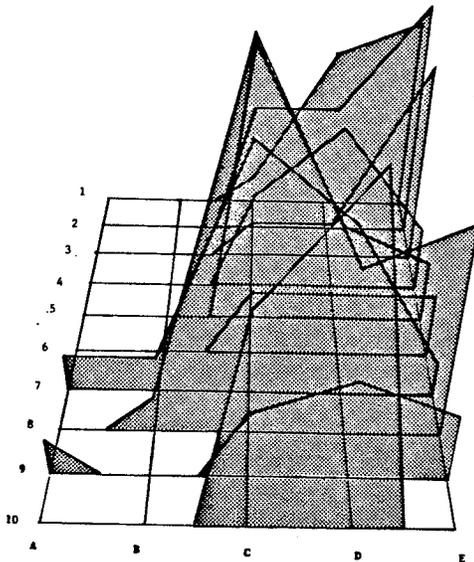
Captures per trap site:

1C=1 4B=2 8B=3 10A=1
 2C=2 6B=2 8C=1 10C=3
 3C=1 6D=1 9C=4 10D=2
 4A=2 7B=5 9D=3 10E=1

**C**

Captures per trap site:

1C=1 3C=1 5C=8 7A=1 8C=10 9E=2
 1D=5 3D=1 5D=3 7B=1 8D=7 10C=6
 1E=6 3E=6 5E=2 7C=7 8E=6 10D=9
 2C=4 4C=3 6C=2 7D=5 9A=1
 2D=4 4D=5 6D=2 7E=1 9C=2
 2E=7 4E=2 6E=2 8B=1 9D=3

**D**

Captures per trap site:

1C=3
 1A=5 2D=1 8A=1
 1C=3 3A=2 9A=4
 1D=3 4B=1 10A=3
 2B=1 7A=1 10B=1

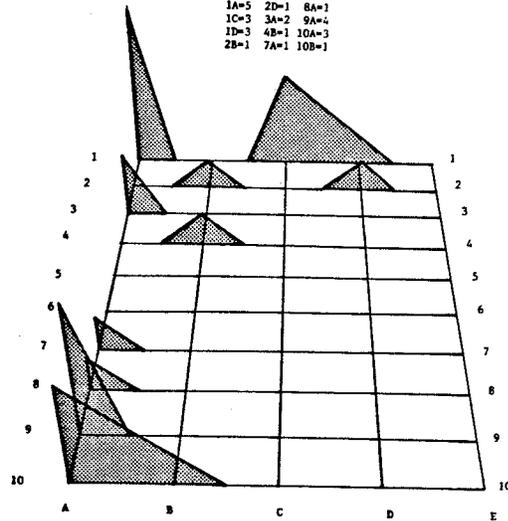
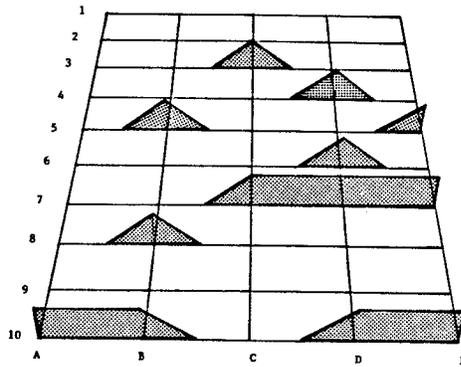


Figure 12. Perspective views of study plot two showing the distribution and frequency of rodent captures in relation to trap sites for the species,

- a) Zapus hudsonius (Zimmerman) in 1980
- b) Spermophilus franklinii (Sabine) in 1980

A

Captures per trap site:
 3C=1 6D=1 8E=1 10E=1
 4D=1 7C=1 10A=1
 5B=1 7D=1 10B=1
 5E=1 7E=1 10D=1



B

Captures per trap site:
 1C=1 3D=3 5E=1 8D=1
 1D=2 3E=1 6E=1 9C=1
 1E=2 4B=1 6E=1 9E=1
 2C=2 5B=2 7C=1 10C=1
 3C=1 5D=1 8B=1 10E=2

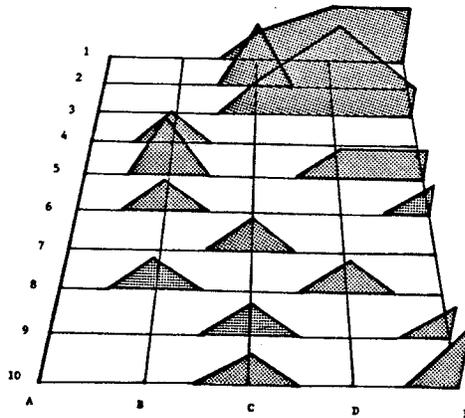
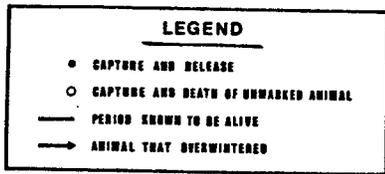


Figure 13. Upper graph of 1979 individual capture histories for Clethrionomys gapperi (Vigors); circles indicate week of capture and lines indicate period of time known to be alive (between capture dates). Lower graph (M.N.A.) represents the minimum number of animals known to be alive during each two week period between 5 May and 22 September.



**TAG
NUMBERS**

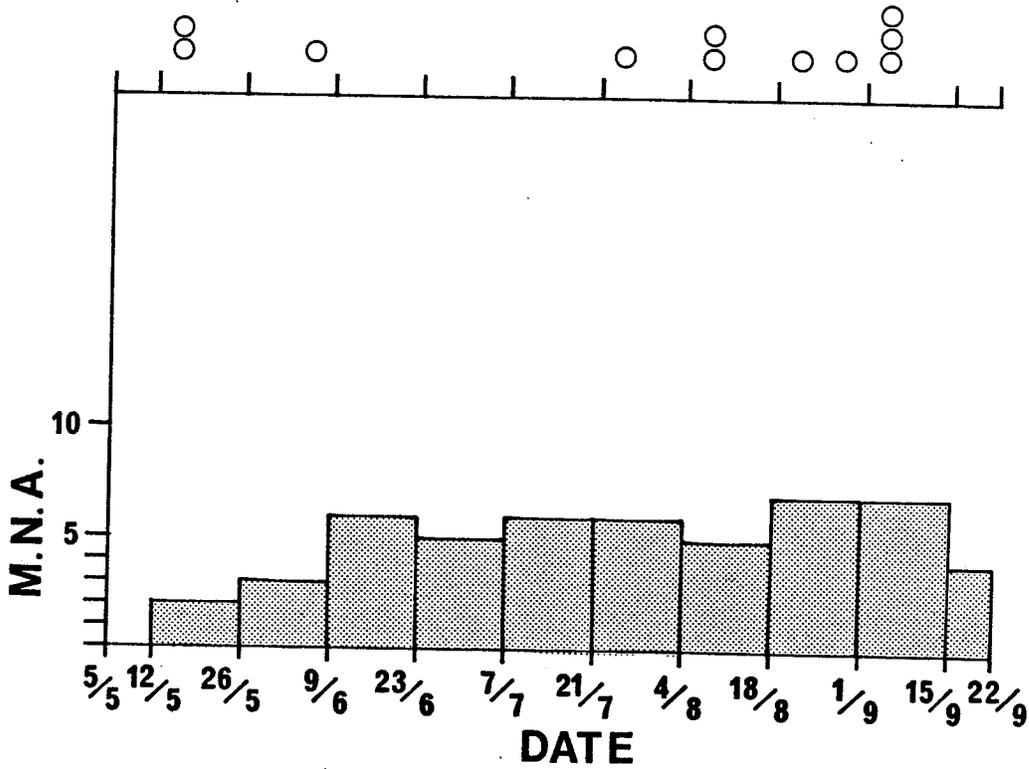
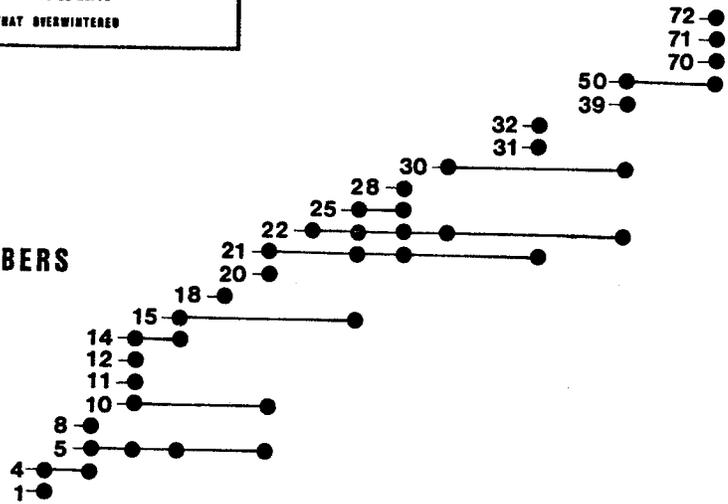
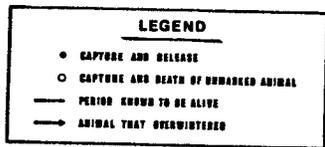


Figure 14. Graph of 1980 individual capture histories for Clethrionomys gapperi (Vigors); circles indicate week of capture and lines indicate period of time known to be alive (between capture dates) between 21 April and 25 August.



**TAG
NUMBERS**

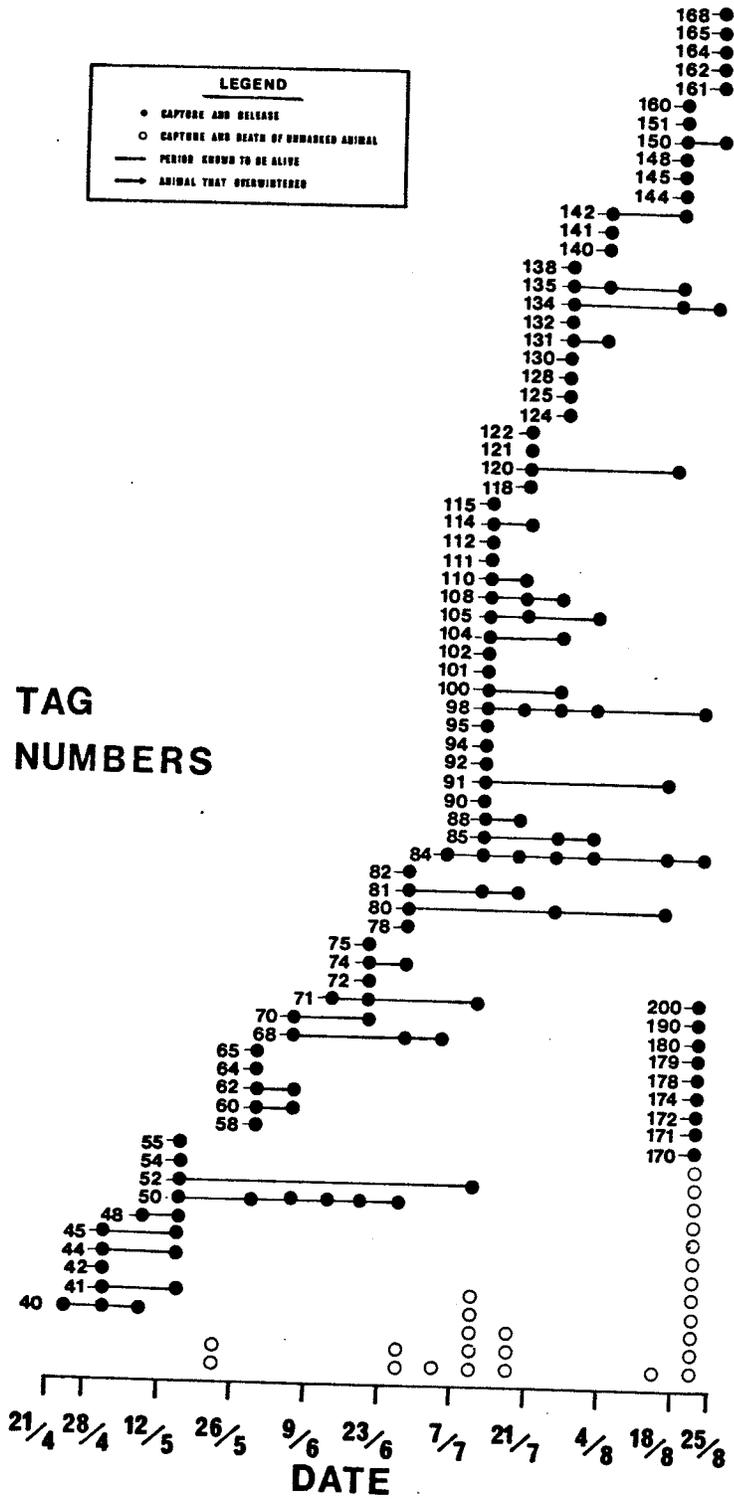


Figure 15. Graph of the minimum number of Clethrionomys gapperi (Vigors) known to be alive in 1980 each two week period between 21 April and 25 August.

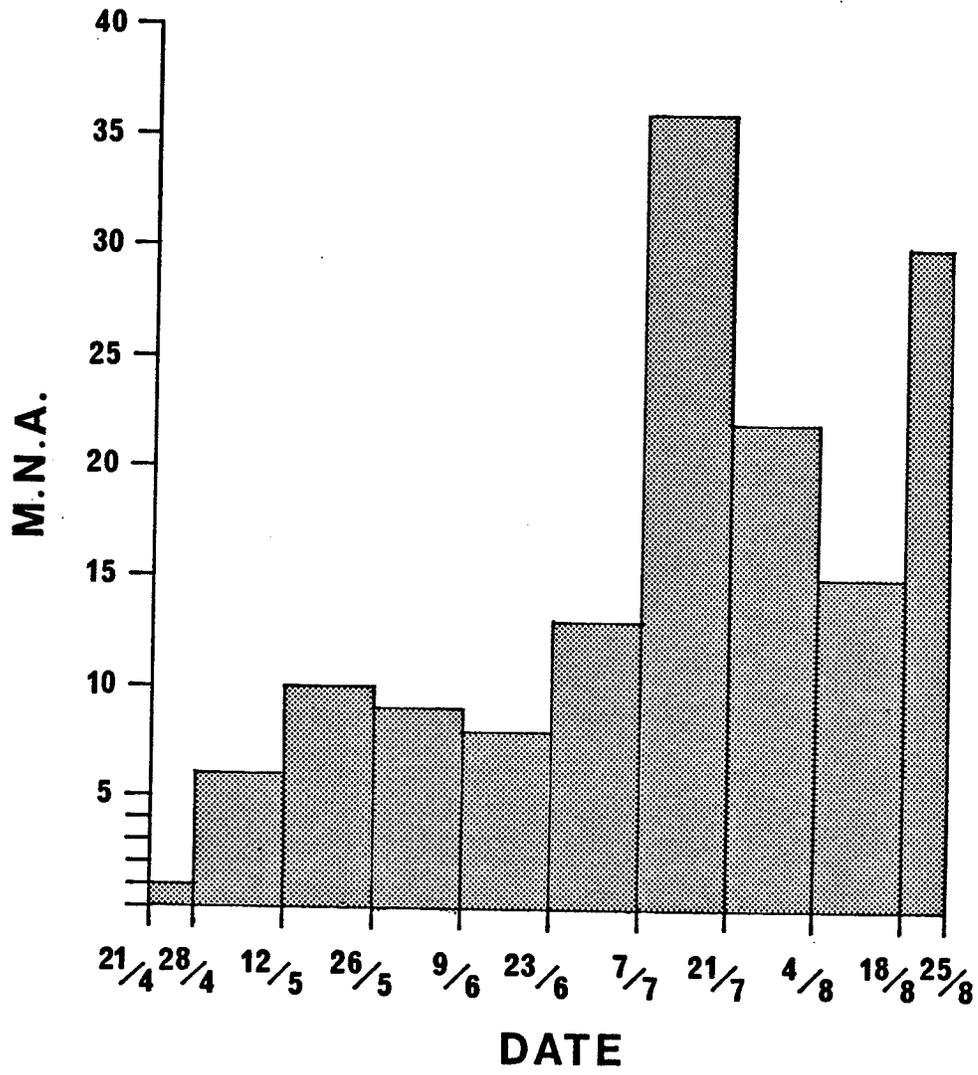
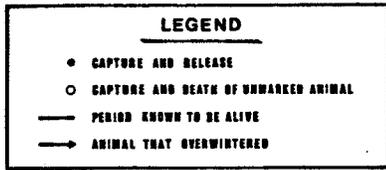


Figure 16. The 1979 capture histories of Microtus pennsylvanicus (Ord) and the minimum number known to be alive (M.N.A.) between 5 May and 22 September. (See Fig. 13 for details).



**TAG
NUMBERS**

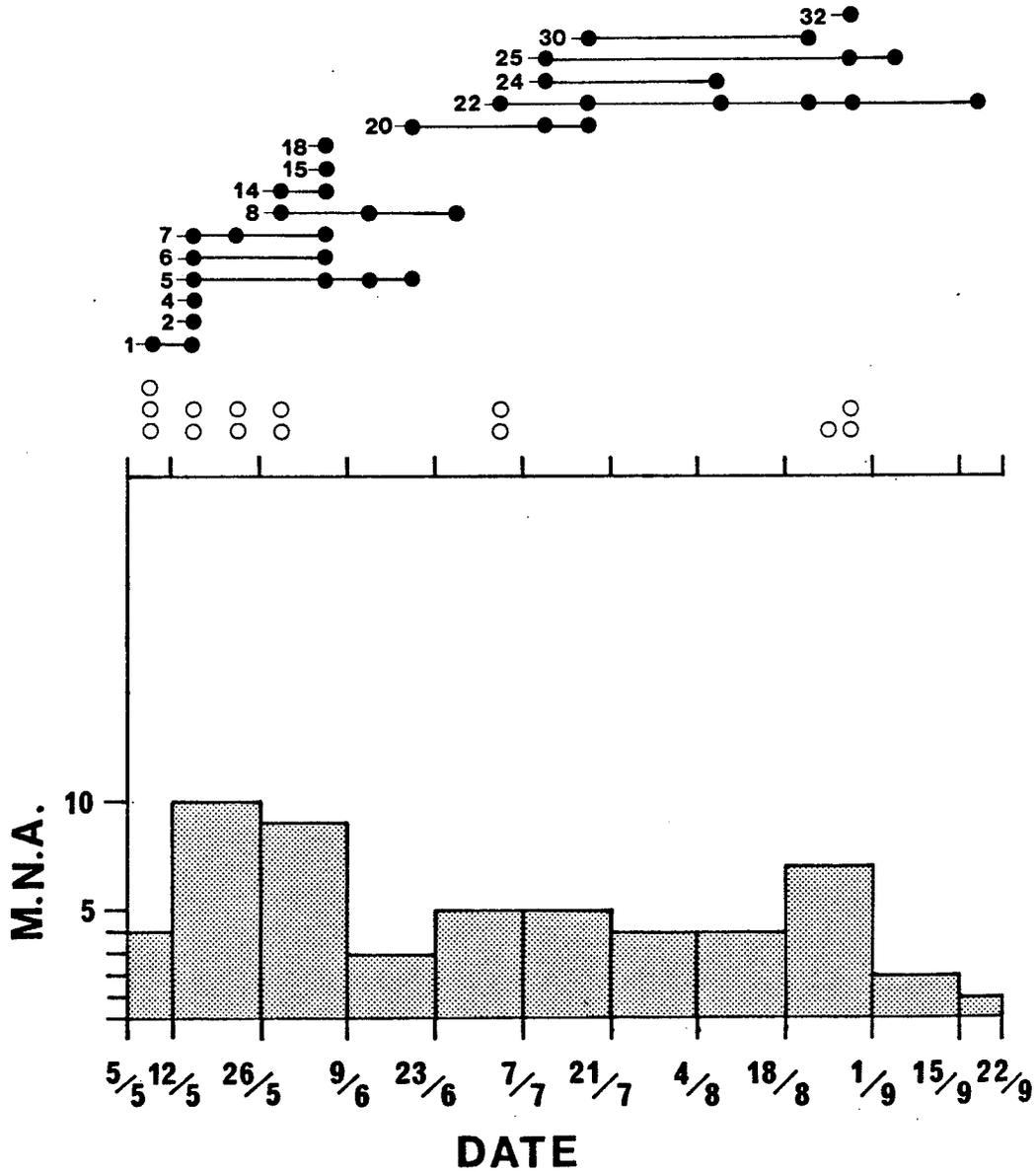
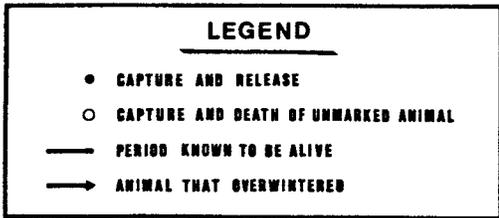


Figure 17. The 1980 capture histories of Microtus pennsylvanicus (Ord) and the minimum number known to be alive (M.N.A.) between 21 April and 25 August. (See Fig. 13 for details).



**TAG
NUMBERS**

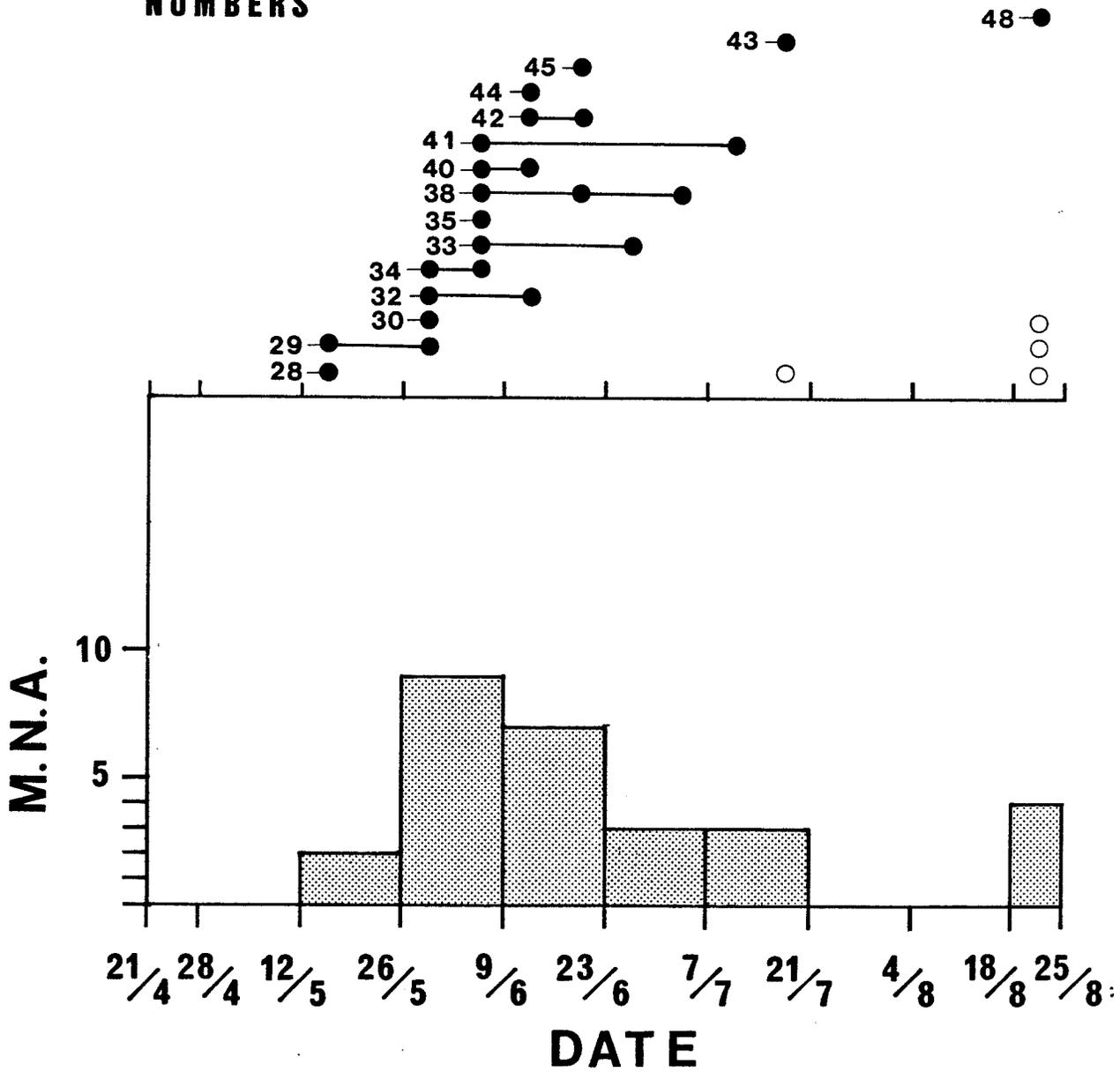
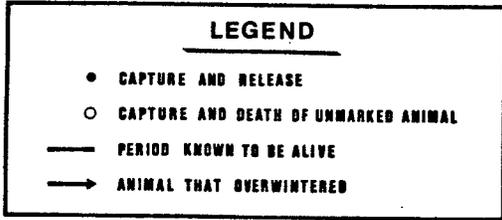


Figure 18. The 1979 capture histories of individual Peromyscus maniculatus (Wagner) and the minimum number known to be alive (M.N.A.) between 5 May and 22 September. (See Fig. 13 for details).



**TAG
NUMBERS**

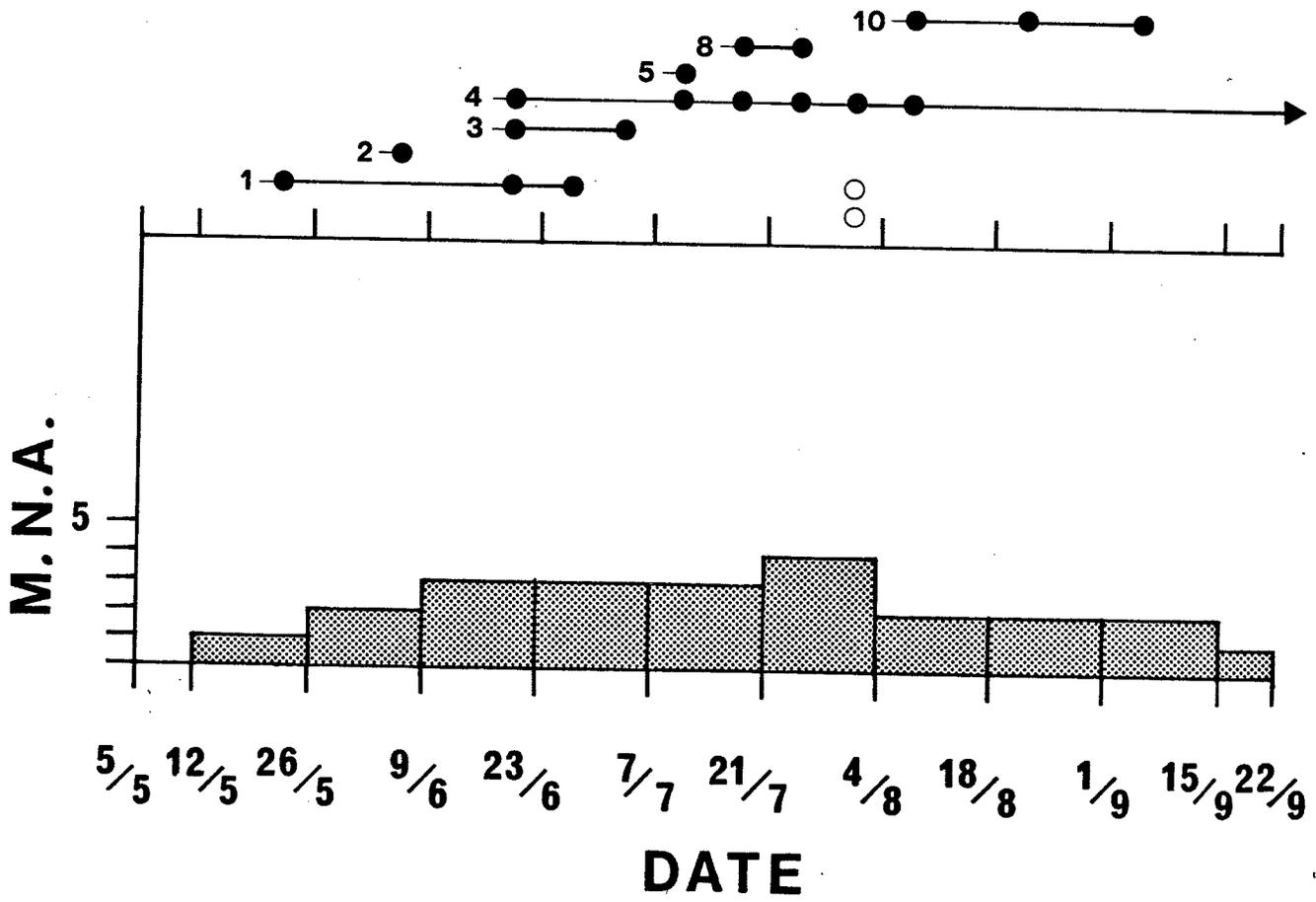
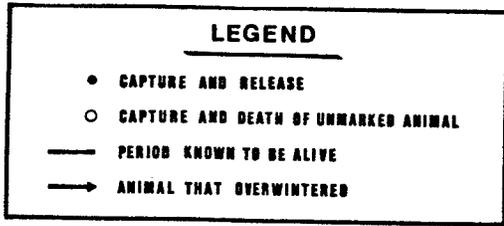


Figure 19. The 1980 capture histories of individual Peromyscus maniculatus (Wagner) and the minimum number known to be alive (M.N.A.) between 21 April and 25 August. (See Fig. 13 for details).



**TAG
NUMBERS**

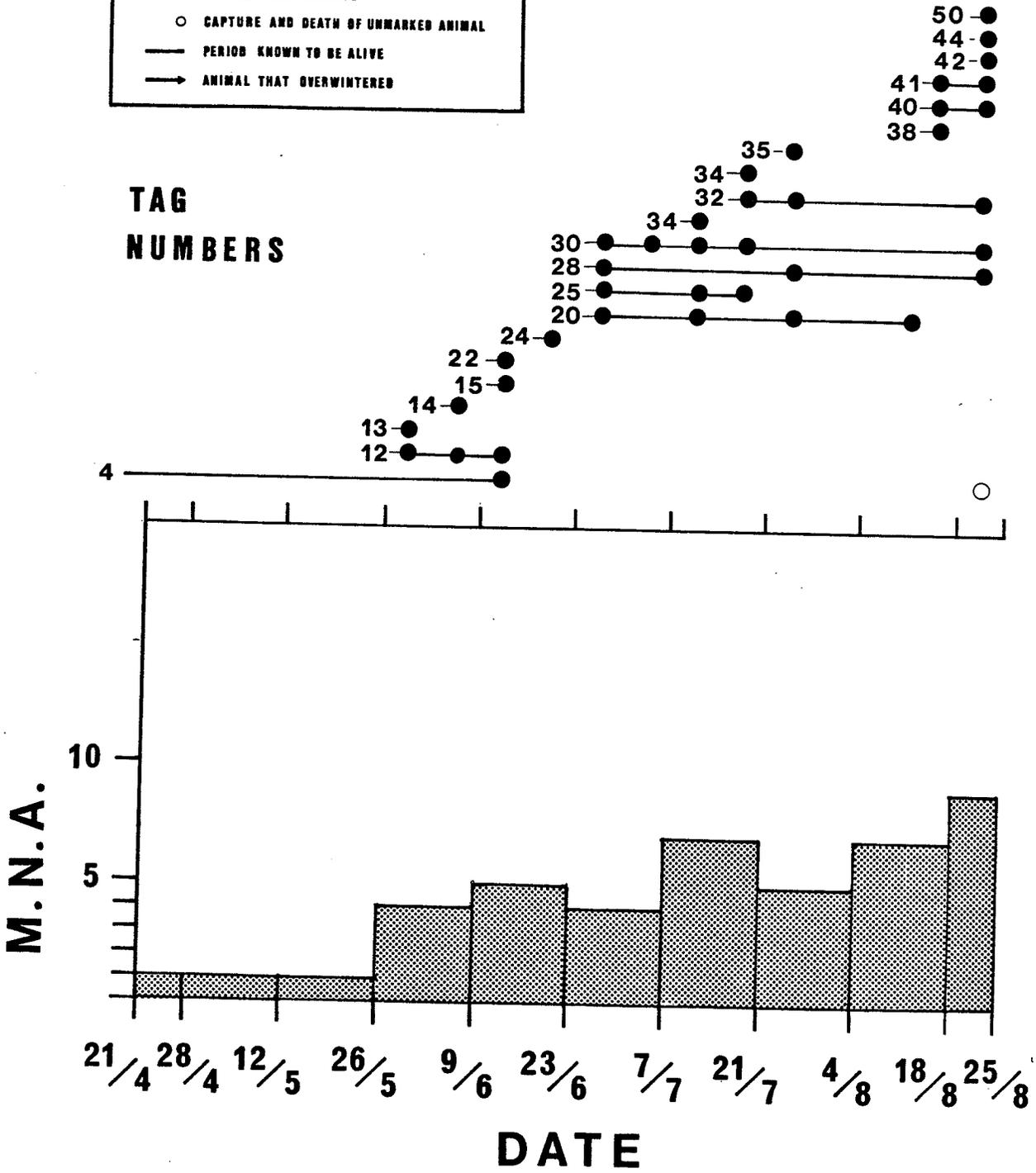
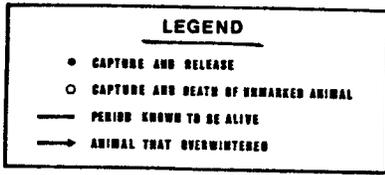


Figure 20. The 1979 capture histories of individual Zapus hudsonius (Zimmerman) and the minimum number known to be alive (M.N.A.) between 16 May and 1 September. (See Fig. 13 for details).



TAG NO.

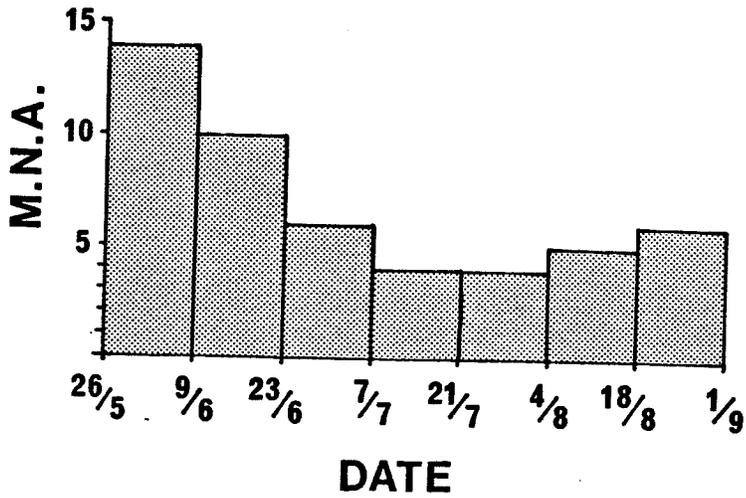
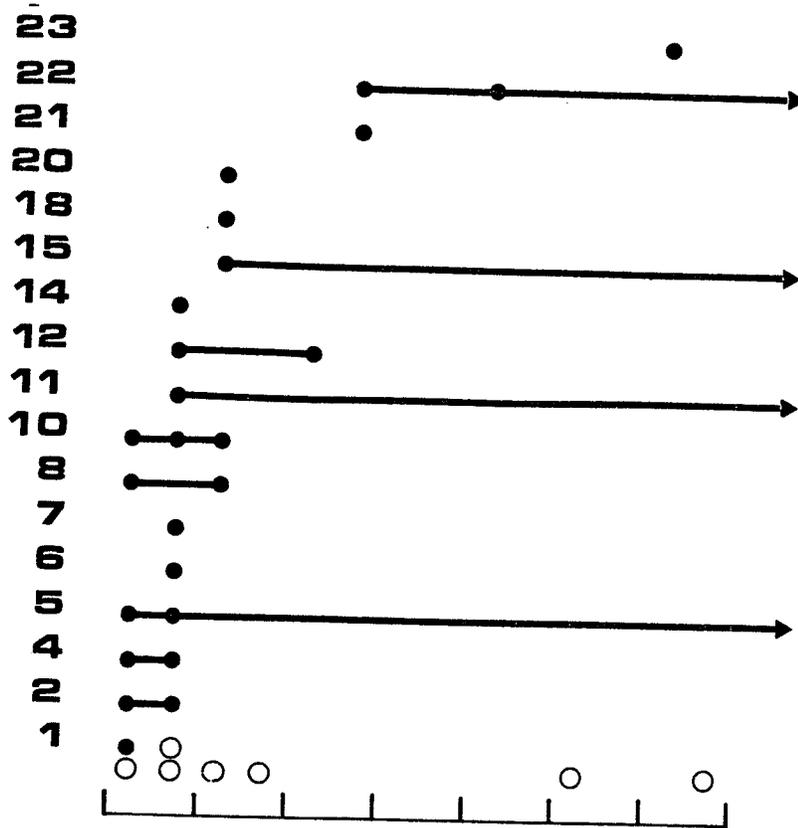
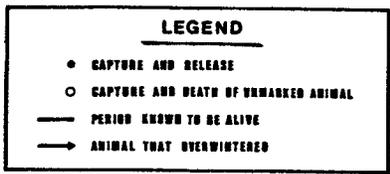


Figure 21. The 1980 capture histories of individual Zapus hudsonius (Zimmerman) and the minimum number known to be alive (M.N.A.) between 28 April and 18 August. (See Fig. 13 for details).



TAG NO.

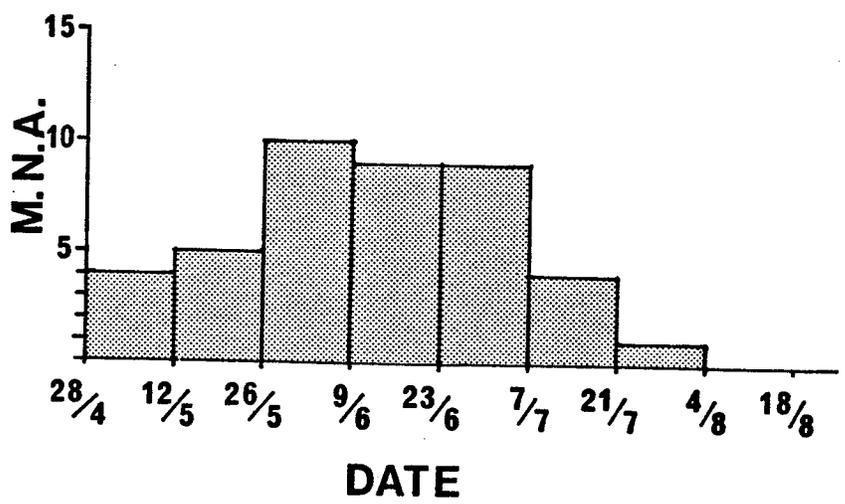
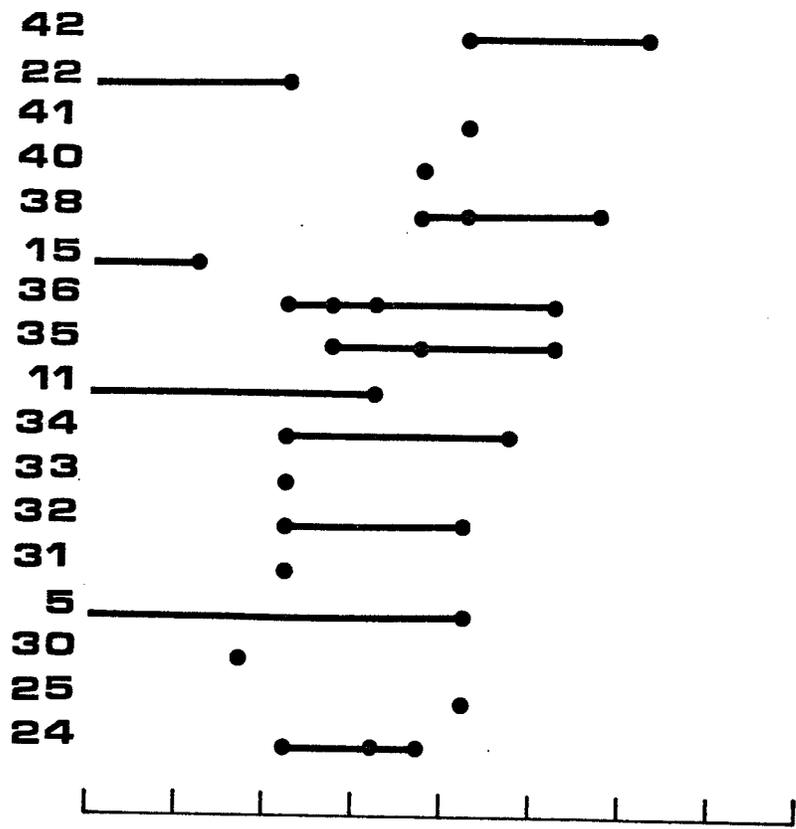


Figure 22. The 1979 capture histories of individual Spermophilus franklinii (Sabine) and the minimum number known to be alive (M.N.A.) between 5 May and 22 September. (See Fig. 13 for details).



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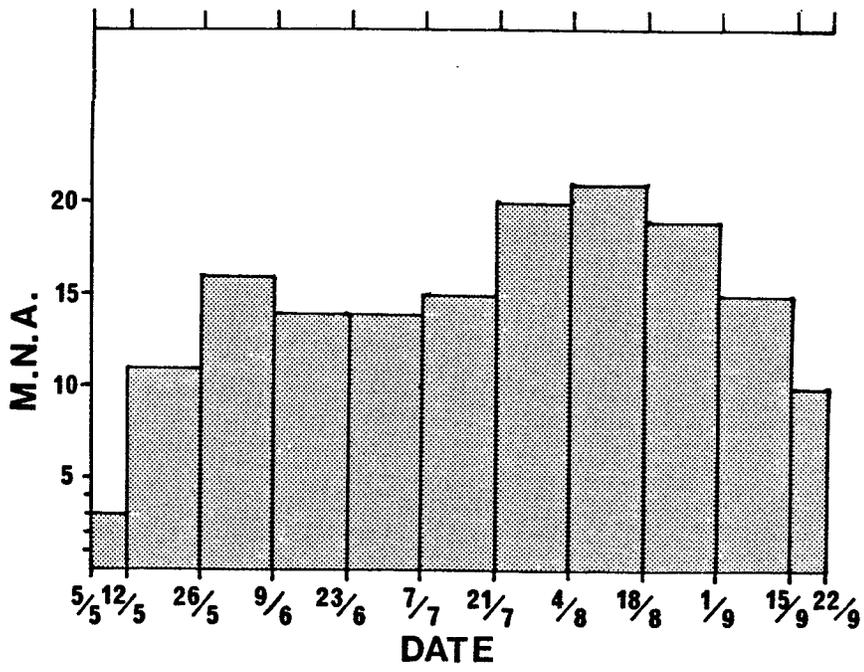
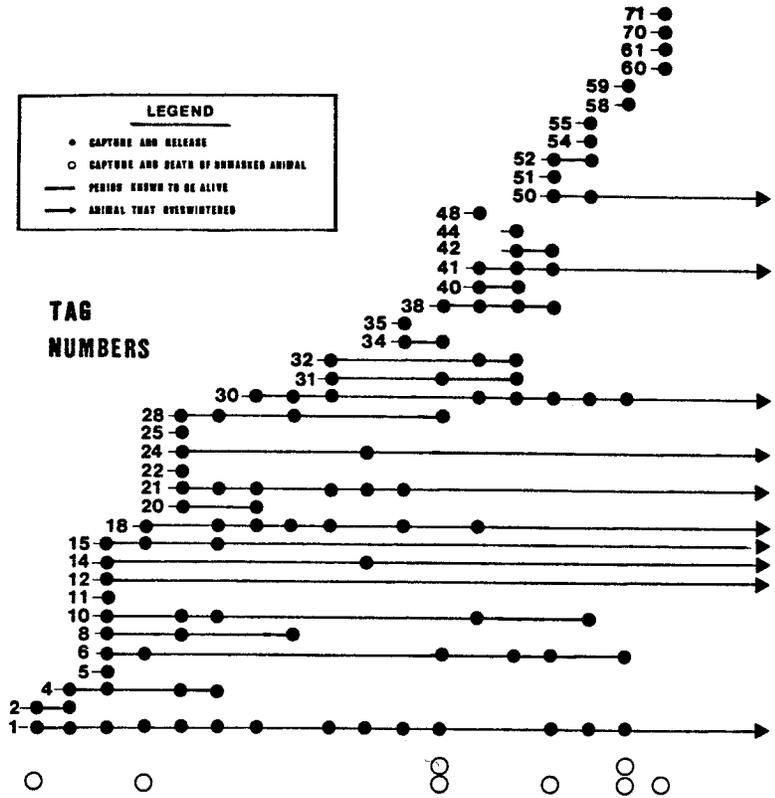


Figure 23. The 1980 capture histories of individual Spermophilus franklinii (Sabine) and the minimum number known to be alive (M.N.A.) between 21 April and 25 August. (See Fig. 13 for details).

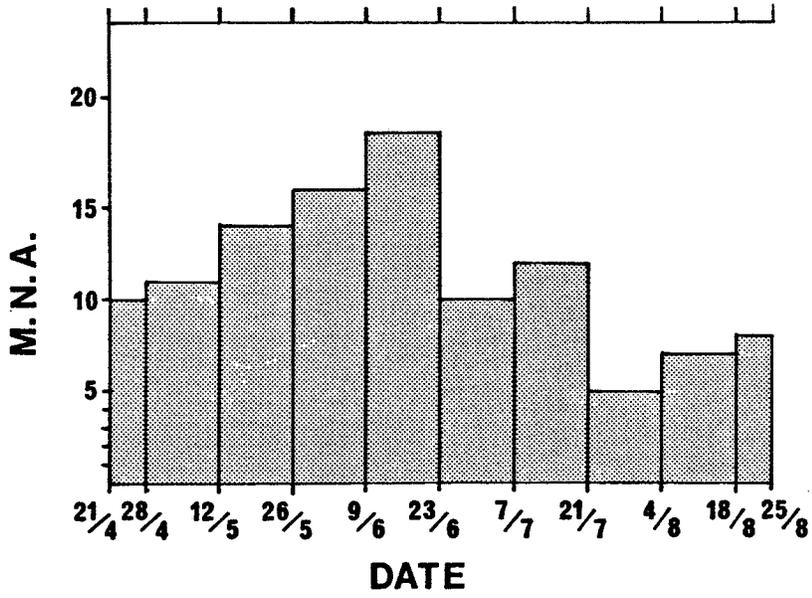
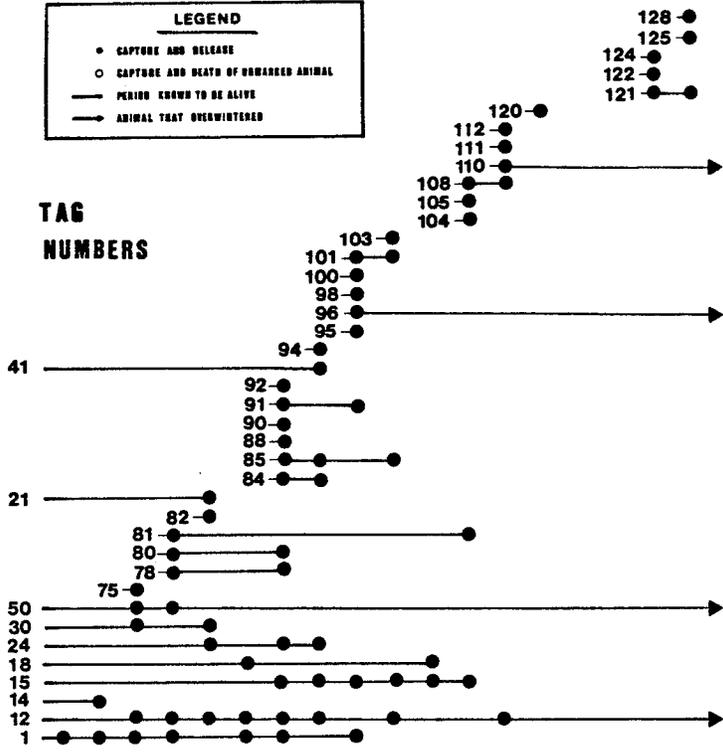


Figure 24. The 1979 seasonal activity of Dermacentor variabilis (Say) larvae (—●—) and nymphs (—■—) expressed as the number collected during each two week period between 26 May and 1 September.

1979

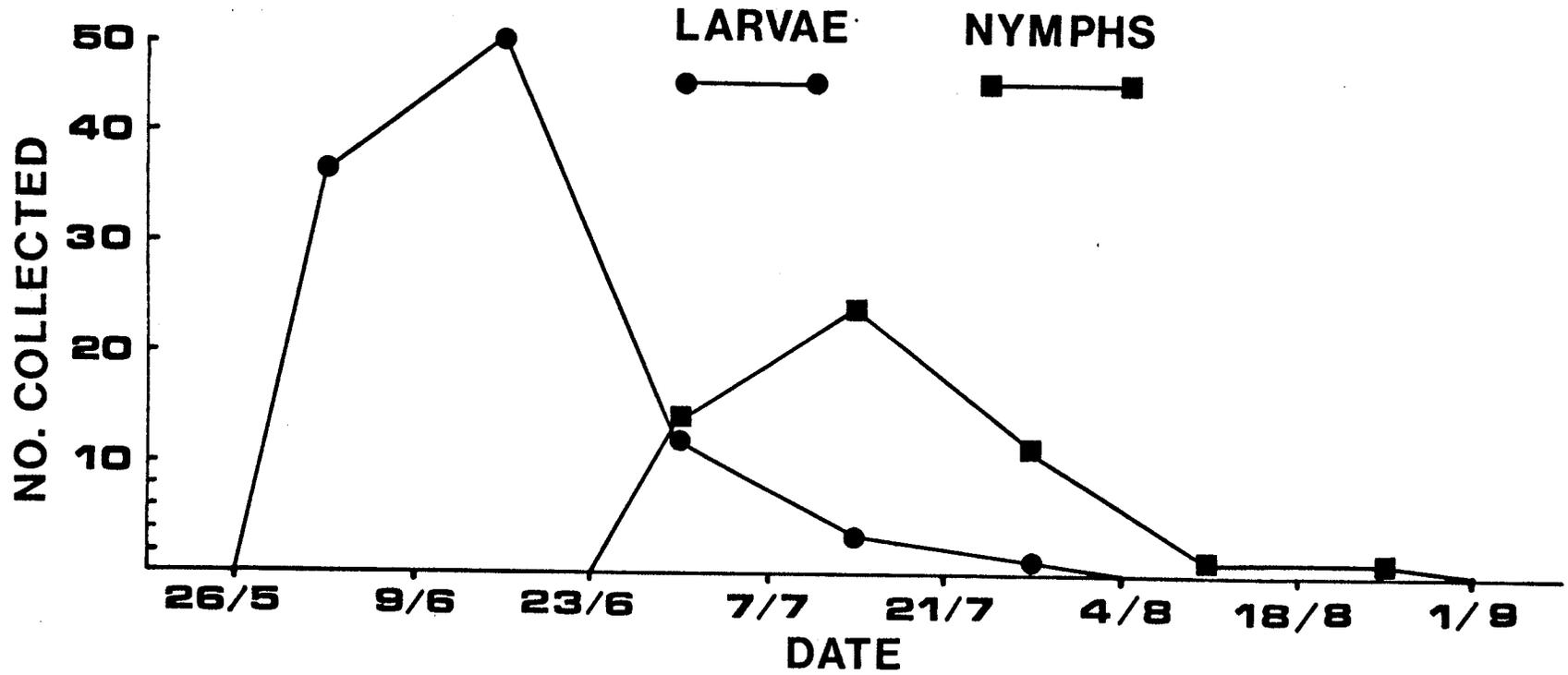


Figure 25. The 1980 seasonal activity of Dermacentor variabilis (Say) larvae (—●—) and nymphs (—■—) expressed as the number collected during each two week period between 28 April and 18 August.

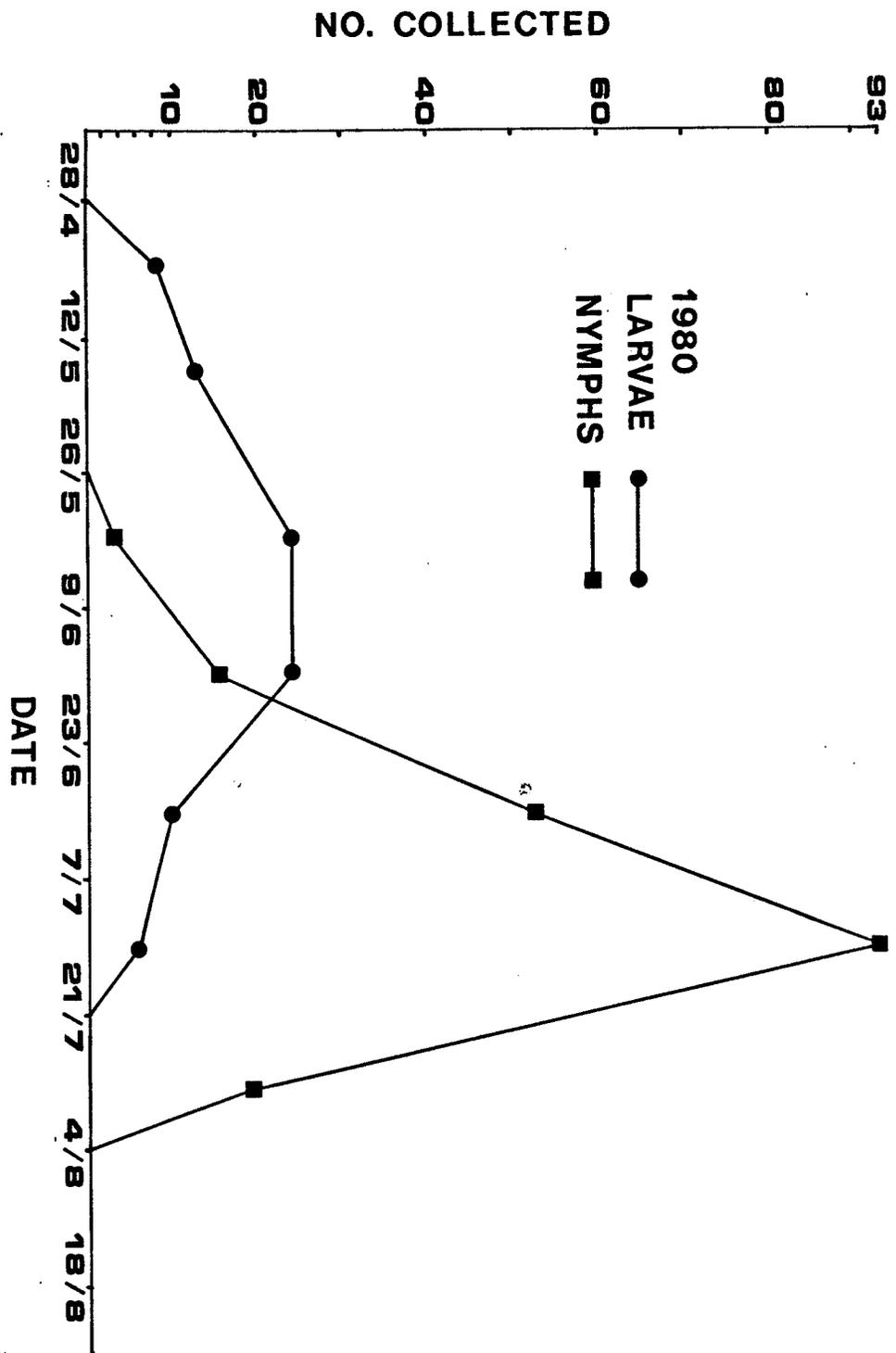


Figure 26. Perspective views of study plot one showing the sites from which Dermacentor variabilis (Say) immatures were collected and the number collected from each site for,

- a) Larvae in 1979
- b) Nymphs in 1979
- c) Larvae in 1980
- d) Nymphs in 1980

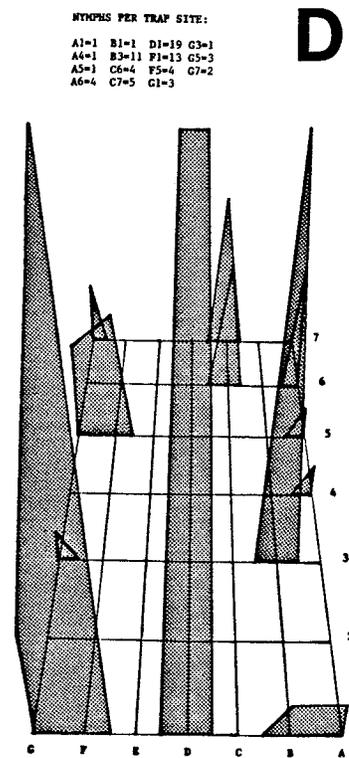
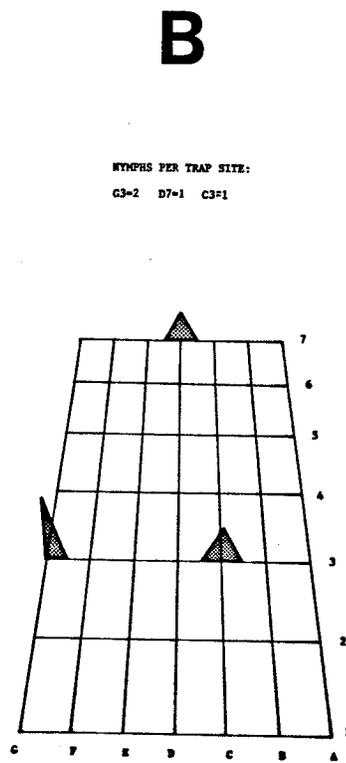
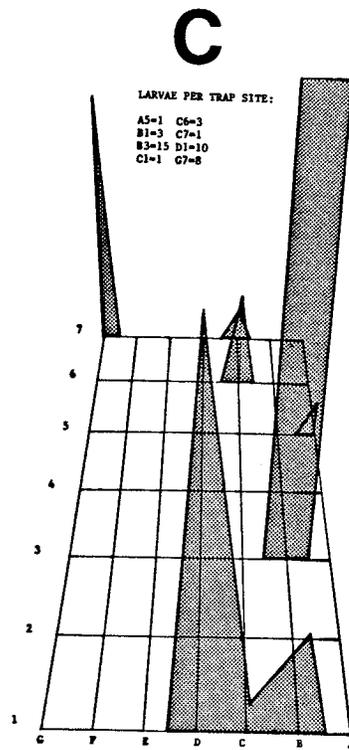
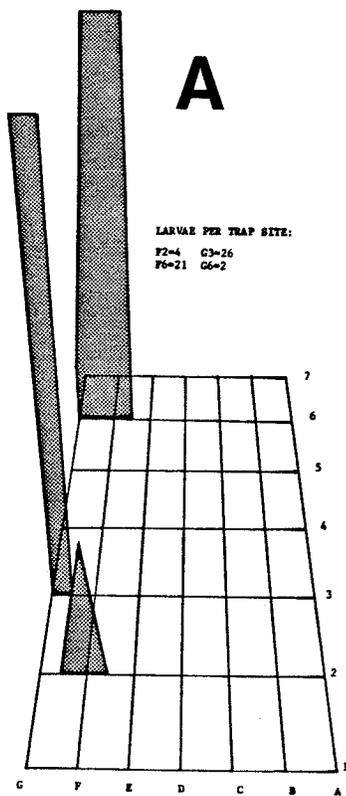
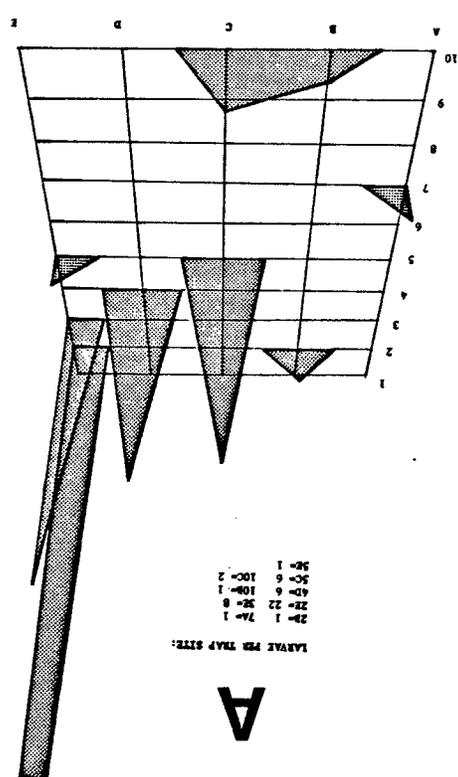
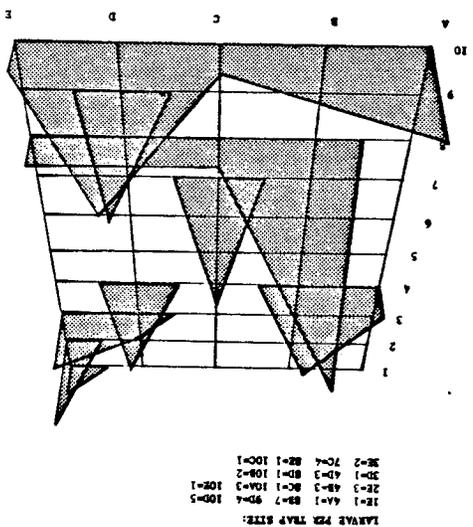
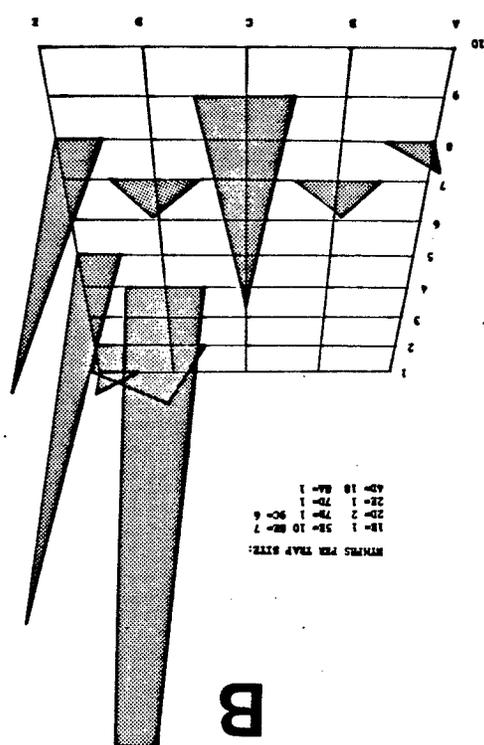
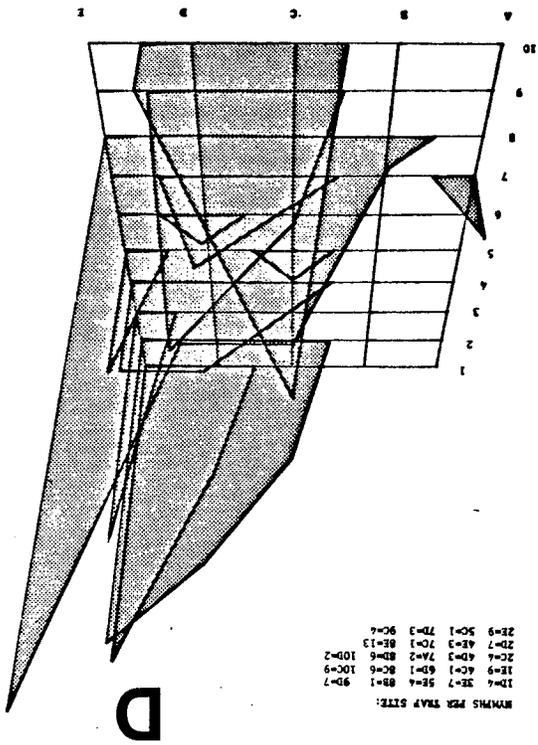


Figure 27. Perspective views of study plot two showing the sites from which Dermacentor variabilis (Say) immatures were collected and the number collected from each site for,

- a) Larvae in 1979
- b) Nymphs in 1979
- c) Larvae in 1980
- d) Nymphs in 1980



APPENDIX I. Plant species associated with various habitats on study plots

Forest habitat

Amelanchier alnifolia
Aralia nudicalis
*Corallorhiza maculata
*Corallorhiza striata
Cornus canadensis
Cornus stolonifera
Corylus cornuta
Crataegus spp.
*Habenaria viridis
Juniperus communis
Lithospermum canascens
Mianthemum canadense
Pedicularis canadensis
Populus tremuloides
Prunus virginiana
Quercus macrocarpus
Rhus radicans
Smilacina racemosa
Smilacina stellata
Viburnum rafinesquianum

Ecotone habitat

Achillea millefolium
Allium stellatum
Amelanchier alnifolia
Arctostaphylos uva-ursi
Asclepias ovalifolia
Aster spp.
Astragalus bisulcatus
Astragalus crassicaarpus
Campanula rotundifolia
Cerastium arvense
Cornus stolonifera
Corylus cornuta
Juniperus communis
Lithospermum canascens
Monarda fistulosa
Oenothera biennis
Pedicularis canadensis
Petalostemon spp.
Populus tremuloides
Prunus virginiana
Rhus radicans
Rosa arkansana
Silene cucubalis
Sisyrinchium montanum
Viola papilionaceae
Viola petatifida
Zizia aptera

Field habitat

Achillea millefolium
Allium stellatum
Anemone patens
Antennaria campestris
Arctostaphylos uva-ursi
Aster spp.
Astragalus bisulcatus
Astragalus crassicaarpus
Campanula rotundifolia
Fragaria spp.
Gaillardia aristata
Geum triflorum
Juniperus communis
Lilium philadelphicum
Lithospermum canascens
Monarda fistulosa
Oenothera biennis
Petalostemon spp.
Potentilla spp.
Rosa arkansana
Sisyrinchium montanum
Solidago spp.
Tragopogon dubius

*Found on plot two only.