THE UNIVERSITY OF MANITOBA

A Study of the Seasonal Population Dynamics of the Ticks *Dermacentor variabilis* (Say) and *Haemaphysalis leporispalustris* (Packard) in a Marshland Habitat

by

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ABSTRACT

Three species of ticks, *Dermacentor variabilis*, *Haemaphysalis leporispalustris* and *Haemaphysalis chordeilis* were found infesting birds and mammals in Delta Marsh, Manitoba. Of the 22 mammal species examined, 12 were infested with *D. variabilis*. *Clethrionomys gapperi* was the most heavily infested. *Microtus pennsylvanicus* was next, then *P. maniculatus* followed by *Z. hudsonius*. The ectoparasitic stages on these rodents were larvae and nymphs. Adults were found on *Spermophilus franklinii* and other larger mammals. Populations of larvae and adult ticks rose rapidly in May and June and then gradually declined in July and August. Mark and recapture estimates were not reliable because of trap-addiction of the rodents in the grids. Relative estimates of rodents revealed the presence of large populations of the rodents and the parasite *D. variabilis*. Rodents from which the ectoparasites had been removed were quickly reinfested. Flagging of vegetation revealed that adult ticks were most numerous at the edge of the woods, less in tall grass and least in the short grass with few in the woods. Flagging samples also revealed populations of 36,000 adult ticks per hectare in 1977 and 148,000 in 1978, a ratio of 1:4. Intensity for all rodent hosts was 3.5 in 1977 and 10.9 in 1978, a ratio of 1:3. The life cycle of *D. variabilis* is probably two years.

In 1977, 19 species of birds were examined for *H. leporispalustris*. Of these, 11 were infested with *H. leporispalustris*. In 1978, 61 species representing 1,727 birds were examined and 25 species (174 specimens) were found infested. There were 14 species of resident birds infested (three ground birds, five shrub birds and four tree species and two species in the Marsh). Eleven species of the non-resident birds were infested (six ground birds, three shrub birds, two tree species). All these birds breed near or north of The Pas. Prevalence was high in the brown thrasher (100%), brown-headed cowbird (100%) and robin (100%). Bird density for Oxbow Wood was 1.1, whereas that for the beach ridge with sandbar willows was 1.3 bird per net hour. Larvae and nymphs were found on birds. Higher infestation was found on ground species than in shrub or tree birds. No adult ticks were found on birds. Leporids were infsted with larvae, nymphs and adults of *H. leporispalustris*.

Spermophilus franklinii and *Sciurus carolinensis* constitute new host records for *D. variabilis.*

Eighteen species of birds represent new host records for *H. leporispalustris*.

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INTRODUCTION

The American dog tick, *Dermacentor variabilis* (Say), is an important pest and in some parts of the United States, a vector of human diseases. Although no records of disease transmission are known in western Canada, in eastern United States this tick was recorded as transmitting Rocky Mountain Spotted Fever, *Rickettsia rickettsi* (Badger, *et al*., 1931; Betram, 1962 and Hoogstraal, 1966). *D. variabilis* also transmits *Pasturella tularensis*, the causative agent of tularaemia. Tick paralysis of humans can also occur (Gregson, 1973).

The rabbit tick, *Haemaphysalis leporispalustris* (Packard) is reported to transmit Rocky Mountain Spotted Fever, tularaemia and Colorado tick fever (a tick-borne virus). These diseases are maintained in the tick population by transovarial transmission (James and Harwood, 1969).

The occurrence of ticks on man in western Canada is of medical interest through blood feeding, skin irritation, and psychological trauma through discovery of ticks on the human body. All these factors are of concern to the departments of tourism and health. Ectoparasitism of livestock is of considerable interest to departments of agriculture. As parasitism is an ecological relationship between populations of biologically distinct organisms (Nutting, 1968; Crofton, 1971a, b), an analysis of the host-parasite interaction, vegetation and environmental factors is essential in order to understand population fluctuations of ticks.

The American dog tick, *D. variabilis* and the rabbit tick, *H. leporispalustris* occur in relatively high densities at Delta Marsh, Manitoba. The large number of hosts, good habitat and adequate moisture, temperature and light probably produce these high densities. To my knowledge *D. variabilis* and *H. leporispalustris* have not been studied at Delta Marsh. In fact the closest studies were carried out in an upland habitat in Nova Scotia, Canada and in the eastern United States of America. Delta Marsh, situated at $50^{\circ}11'$ latitude and $98^{\circ}19'$ longitude is in the northern limits of *D. variabilis* range. At this latitude, climatic conditions are rigorous and become more severe as one moves further north.

Basic biological and ecological information are needed to evaluate population dynamics of *D. variabilis* and to a lesser extent *H. leporispalustris* in a north temperate climate in a marshland ecosystem.

The objectives of this study were:

(a) To determine species of ticks occurring at Delta and their hosts;

(b) To determine seasonal population dynamics of *D. variabilis* on their mammalian hosts;

(c) To determine seasonal population dynamics of *D. variabilis* on vegetation;

(d) To evaluate factors affecting growth, and time required for development of larvae, nymphs and adults of *D. variabilis*; and

(e) To determine seasonal dynamics of *H. leporispalustris* on birds and rabbits.

LITERATURE REVIEW

I. DISTRIBUTION

A. *D. variabilis*

The genus *Dermacentor* has about 30 species distributed in Europe, Asia, Africa and North and Central America. Arthur (1960) gave a systematic account of the genus, and Cooley (1938) dealt with species in the United States.

In North America *D. variabilis* is widely distributed east of the Rocky Mountains in areas less than 500 m above sea level (Fig. 1). It is primarily a tick of shrubby clearings, roadsides, and flood plains in deciduous forests of eastern N. America (Smith, *et al.*, 1946; Bequaert, 1946; Gregson, 1956; Rapp, 1960; and Sonenshine, *et al.*, 1966). Heavily forested areas have fewer ticks than grassy and bush-covered areas (Bishopp and Trembley, 1945).

In Canada Gregson records this species across southern Canada from Nova Scotia (2 sites), Ontario (11 sites), Manitoba (1 site) to eastern Saskatchewan (6 sites), where it shares a natural boundary with *D. andersonii* (Stiles) (Bishopp and Trembley, 1945). This boundary continues south to Montana, Wyoming, Colorado, and New Mexico (Cooley, 1938). Prairie records, including Manitoba, are from

Figure 1. Map of the distribution of *D. variabilis*, *H. leporispalustris* and *H. chordeilis* in North America.

d = *D. variabilis*
x = *H. leporispalustris*
c = *H. chordeilis*

aspen-parklands. In Ontario records are from the Niagara section of the deciduous Great Lakes-St. Lawrence forest (Wilkinson, 1967). In Nova Scotia heaviest infestations occur in the mildest and most humid regions such as the Acadian forest (Putman, 1940).

In the U.S.A. *D. variabilis* is found everywhere except in the state of Washington, the Rocky Mountain and the inter mountain region. Its populations are relatively high on islands along the east coast, on Cape Cod, Long Island and southward along the coast (Bishopp and Trembley, 1945). Bishopp and Smith (1938) reported that it is less abundant on the north side than on the south side of Cape Cod. It has been reported from Alaska, Colorado, Arizona and New Mexico. It is also common in the Gulf Coast states, especially Florida and Texas (Bishopp and Trembley, 1945). As this species depends on small rodents as hosts for the immature stages, the distribution of host animals is an influential factor on the incidence of the tick.

B. *H. leporispalustris*

The genus *Haemaphysalis* is cosmopolitan and has about 90 species (Hoogstraal, 1967). *H. leporispalustris* has the widest distribution in North America ranging from Alaska, the southern portions of the provinces of Canada and south into Mexico (Fig. 1). Specimens have been collected from every state in the U.S.A. except South Dakota, Nebraska, Missouri, Arkansas, Delaware, Kentucky and West Virginia (Bishopp and Trembley, 1945), but there is no reason to believe that it does not exist in these states. Most ticks from birds or from their nests are recent transients from the south but some of them may have overwintered in Canada. Gregson (1956) recorded *H. leporispalustris* from British Columbia (10 sites), Alberta (4 sites), Saskatchewan (3 sites), Manitoba (3 sites), Ontario (8 sites), New Brunswick (4 sites), Nova Scotia (2 sites) and Newfoundland (1 site).

C. *H. chordeilis*

H. chordeilis is a North American species found in the eastern and southern parts of the United States (Fig. 1). In Canada it is found from east to west. Gregson (1956) reported *H. chordeilis* in British Columbia (8 sites), Alberta (3 sites), Saskatchewan (1 site), Manitoba (3 sites), Ontario (2 sites) and New Brunswick (1 site). As this species can be easily confused with *H. leporispalustris*, particularly the immature stages, it is possible that this has affected the records of occurrence in the literature and hence the known distribution of H. chordeilis. It may, therefore, be more widely distributed than is reported. Bishopp and Trembley (1945) reported that the species does not thrive in drier portions of the country.

II. HOST RECORDS

Host records of D. variabilis (Appendix I) show that the tick has a wide variety of hosts. Of the 55 host species listed, small mammals represent over 40%. Mice and voles are infested with larvae and nymphs but in one case an adult tick was found on a meadow vole (Appendix I). Muskrats, which are the largest and most nearly aquatic of the family of rodents, were infested with larvae, nymphs and adult ticks (Bishopp and Trembley, 1945). Most of the larger mammals carry adult ticks but occasionally a nymph may be found. Voles were reported to be the most heavily infested of the lower mammals. There are no records of bird hosts.

H. leporispalustris (Appendix II) host records show a very high number of 98 host species. Though this tick is commonly known as the rabbit tick, birds represented over 70% of the hosts listed. Infestation levels were much higher on rabbits, averaging 450 ticks per host for rabbits examined in most studies, and a high of 2880 ticks on a single individual was reported (Cooley, 1932). Man is also recorded as a host (Gregson, 1956). Among the birds, eastern and western meadowlarks were the most heavily infested, with a high of 243 individuals (Bishopp and Trembley, 1945).

H. chordeilis, though commonly known as the bird tick, is known to occur on 18 bird species out of a host list of 26 (Appendix III). The record includes man, cattle and horses. Meadowlarks were the most heavily infested, with a high of 194 ticks on a single host (Bishopp and Trembley, 1945).

III. TICK BIOLOGY

A. Life Cycle

The developmental cycle of *D. variabilis* (Appendix IV) as reported by Hooker, *et al*. (1912), Hadwen (1913), Bishopp and Smith (1938), Smith, *et al*. (1946) and Sonenshine and Atwood (1967), consists of the following stages; egg, larva, nymph, and adult. After dropping from the host, the adult female commences oviposition. Eggs are laid on the ground, in burrows, crevices, nests and cracks. With abundant moisture, vegetation and favourable temperature eggs will hatch within 35 days. Larvae remain on the ground or on low growing vegetation until a host, usually a small rodent, passes by. Larval engorgement lasts 3-12 days (average 4 days) after which the larva drops to the ground and moults to a nymph in about seven days. Nymphs feed on rodents or leporids for 3-11 days (average 6 days). The metamorphosis to adult takes three weeks to several months depending on temperature. Adult ticks prefer larger mammals though domestic dogs (James and Harwood, 1969) are their most favoured hosts. After attachment females become engorged in 6-13 days. Mating takes place on the host with the male seeking out the attached female. Mating increases the rate of feeding in the female (Gregson, 1944). When fully engorged, the female drops to the ground, oviposits and dies. Under favourable conditions the life cycle from egg to adult may require up to three months, but as both adults and immature ticks have remarkable longevity in the absence of suitable hosts, the life history may be greater than two years. Adults, nymphs and larvae have been maintained for as long as 273, 377 and 988 days respectively (Bequaert, 1946).

B. Attachment and Feeding

A blood meal is essential for the production of eggs. Although *D. variabilis* has a wide range of hosts, marked differences were noted in previous studies, of the degree of utilization of different wild vertebrates as hosts. Sonenshine and Atwood (1967) reported that larvae and nymphs fed most readily on *Microtus pennsylvanicus* (Ord.) and less on *Peromyscus maniculatus* (Rafinesque) and *Rattus norvegicus* (Berkenhout). Drummond, *et al*. (1971) reported an average weight of 0.398 gm for adults fed on cattle while Nagar (1968) reported 0.465 gm for ticks fed on domestic rabbits and Amin (1969), 0.601 gm for those fed on domestic dogs. Factors which stimulate ticks to feed are important aspects of their ecology. Odour and grooming influence attachment (Sonenshine and Atwood, 1967).

C. Oviposition

Preoviposition periods for female *D. variabilis* are 3-5 days (Hooker, *et al*. 1912), 3-24 days (Bishopp and Smith, 1938), 3-5 days (Sonenshine and Tigner, 1969), and ranged in the literature as widely as 2-24 days.

The oviposition period varies from 10-28 days (Drummond, *et al*. 1971) with egg production reported as 4568 (Hooker, *et. al*. 1912), 5956 (Bishopp and Smith, 1938), 4156 (Sonenshine and Tigner, 1969), and the range, 2523-7216 (Nagar, 1968).

Most studies recorded peak oviposition of 381-522 eggs between days 2-8 (Drummond, *et al*. 1971). Heavier female *D. variabilis* lay more eggs and require more time to complete oviposition (Nagar, 1968). Tick eggs withstand harsh environmental conditions, but they generally do not withstand dessication well (James and Harwood, 1969).

In a study on the oviposition of *Boophilus microplus* (Canestrini) Bennett (1974) found that engorged females with small size (< 100 mg) were not as efficient in converting the blood meal into eggs, but that the ticks in the range of 100-370 mg had a remarkably uniform efficiency of conversion. Nagar (1968), Amin (1969) also reported that heavier *D. variabilis* laid more eggs. A similar relationship was reported for the following tick species: *Hyalomma anatolicum anatolicum* (Koch) (Snow and Arthur, 1966); *Rhipicephalus sanguineus* (Sweatman, 1967); *H. bispinosa* (Hoogstraal *et al*. 1968); and *D. albipictus* (Drummond, *et al*. 1969).

Bennett (1974) reported that oviposition in *B. microplus* was completed in 16 days with 95% of eggs laid by day 10. Eggs laid on the 1st day had low viability while eggs laid from 2-12 days had a hatch rate of 75-100%. Viability then decreased and 0-10% of eggs laid in the last 4 days hatched. This pattern of a maximum number of eggs laid during the first few days and a decline thereafter was observed in *D. variabilis* and other tick species (Nagar, 1968) but little mention is made of their viability.

D. Parthenogenesis

Parthenogenetic reproduction was reported for several Ixodid tick species (Oliver, 1971). Bremmer (1959) found that parthenogenesis was the normal method of reproduction in a strain of *H. bispinosa* Neumann. Stone (1963) reported parthenogenesis in *B. microplus* (Canestrini) from Australia. Nagar (1967) reported parthenogenesis in *D. variabilis* but did not investigate the fate of the larvae derived in this manner. Gladney and Dawkins (1971) made further investigations on *D. variabilis* parthenogenetic reproduction. Their study indicated that eggs were laid by unmated *D. variabilis* females and that there was a 1.5% hatch from these eggs, compared to 75.9% from mated females. They also reported that most of their parthenogenetically produced larvae survived for 2-3 days. These parthenogenetically produced larvae did not attach to a host while those from mated females attached and fed with no mortality. Larvae from mated females also lived longer than 3 days. Gladney and Dawkins (1971) concluded that parthenogenesis in *D. variabilis* in nature did not occur to any significant extent.

E. Sex Ratio

There are few reports in the literature on sex ratio. Sonenshine, *et al*. (1972) reported that males (64.4%) outnumbered females (35.6%) while Gladney and Dawkins (1971) reported that most of the hosts that they examined carried 2 or 3 females more than males. Smith (1974) stated that in any population of sexually reproducing animals, natural selection tends to favour males at birth and, because of the higher death rate during development, they become less numerous, resulting in equal sex ratios, and by adulthood it may favour either male or female. Ticks recovered from vegetation samples from spring to late summer show decreasing numbers of males (Smith, *et al*. 1946; Sonenshine, *et al*. 1966; Dodds, *et al*. 1969 and McEnroe, 1971).

F. Overwintering Diapause

Few studies have been conducted on tick diapause, but there are many reports by entomologists on insect diapause. Belozerov (1971) reported that seasonal delay in moulting of engorged larvae of *Ixodes ricinus* was described by Beinarowitch in Russia as early as 1907.

He also reported that five categories of diapause as described by Alfeev; (a) a non-activity of unfed ticks, (b) a delay of engorgement, (c) a delay of metamorphosis in engorged larvae and nymphs, (d) a delay of oogenesis in engorged adult females, and (e) an egg diapause, causing a delay in embryogenesis. Belozerov (1971) classified diapause in ticks into two basic types, i.e., behavioural and morphological, the former for unfed ticks and the latter for engorged ticks. Behavioural diapause is characterized by lack of aggressiveness by unfed ticks. Diapause of this type occurs in larvae and nymphs of North American ticks *D. variabilis*, *D. albipictus*; the European *I. ricinus*, and adults of *D. variabilis* and Eurasian ticks *D. marginatus* and *D. pictus*. Morphogenetic diapause is characterized by a delay of metamorphosis in the immature stages and a delay of oogenesis in adult females. The reactions of ticks to day-length are of importance in the regulatory mechanisms of both types of diapause (Belozerov, 1971). Smith and Cole (1941) showed the dependence of activity of larvae and nymphs of *D. variabilis* on day-length. Belozerov (1971) reported that other studies by himself on oogenesis in adult *D. marginatus* and by Loew in the control of metamorphosis of *I. ricinus* larvae showed that diapause in Ixodid ticks is regulated photoperiodically.

Babenko (1967) found that the photoperiod affected larvae and nymphs of *I. persulcatus*. Khalil (1976) reported that during the fall-winter facultative diapause in nature, female *Argas* (*Persicargas*) *arboreus* Kaiser, Hoogstraal and Kohls, delay oviposition until spring. Photoperiodic regulation interfered with initiation or termination of diapause. Khalil (1976) further suggested that, as in many insect studies, diapause induction in *Argas* (*P.*) *arboreus* is associated with the synthesis and or activation of an inhibitor, i.e., a diapause hormone. Andrewartha, *et al.* (1974) suggested that a hormone is generally present in insects with obligate and facultative diapause.

G. Questing Behaviour

The initiation of questing activity of *D. variabilis* is associated with a positive photo response, and termination of activity with desiccation (McEnroe and McEnroe, 1973). These stimuli, under dry conditions, combine to produce a diurnal cycle of activity (McEnroe, 1971). In the absence of desiccation ticks will remain questing. During a period of continuous fog (McEnroe, 1971) marked ticks remained upon the grass during the night and were questing the following day. Questing behaviour was shown to be regulated by the tick's water balance. As water approached 5% of the tick's initial weight 50% of the ticks were switched from questing into the non-questing behaviour state (McEnroe and McEnroe, 1973).

Solar radiation was also implicated in the questing activity of *D. variabilis* and overcast, rainy days depressed tick questing activity (Sonenshine, *et al*. 1966; Atwood and Sonenshine, 1967). Field observations on *D. variabilis* established 5°C as the lower air temperature threshold for activity (Hall and McKiel, 1961). Semtner, *et al*. (1971) found that rising temperature during the activity season depressed questing activity of *Amblyomma americana* L. Tick activity on the soil surface, but not questing, occurs when the soil temperature reaches 10°C (Wilson, *et al*. 1972). The optimum range for *D. variabilis* lies between 15°C and 25°C for questing behaviour (McEnroe, 1972). Saturated weight of the ticks varied with temperature, with maximum saturation weight at 20°C and a decrease in weight between 5°C and 40°C.

Soil temperatures, even under saturated conditions, are more stable than those of the air (Mackinney, 1929 ; Geiger, 1965) and can regulate questing response (McEnroe and McEnroe, 1973). Adult ticks leave the microclimate at ground level and climb to the tip of a blade of grass where they are exposed to ambient conditions. Lees (1964, 1969) proposed that for *I. ricinus* water loss occurs during questing and an uptake of water vapour occurs while at ground level.

Questing activity results in an aging effect which reduces the tick's resistance to water stress and in the terminal stage the tick can only maintain its water balance and survive under continuous saturated conditions (Lees, 1969). There is restricted movement in the field, and laboratory experiments with sticks, showed that ticks were found on the same stick for the greater part of the questing period (McEnroe and McEnroe, 1973; Sonenshine, *et al*. 1966). Ticks are normally found on grass stems at heights above 15.24 cm from the ground. They hang, head down, with the third pair of legs gripping the grass blade and the remaining three pairs spread and in readiness for gripping hold of a passing host. Photostimulus is necessary for initiation of questing but darkness has no immediate effect on its termination (McEnroe and McEnroe, 1973).

Records of nymphal activity and moulting indicate that adults emerging late in the season do not become active until the following spring (Smith, *et al*. 1946; Sonenshine, *et al*. 1966). It is thought that this non-questing response must have been determined by environmental conditions in the nymphal stage (McEnroe and McEnroe, 1973). Overwintering is, therefore, required to release questing behaviour the following spring. Studies on *D. andersoni* showed that adults emerging late in the season do not go into hibernation but wander on the soil surface. They do not show questing behaviour at this time even under favourable conditions. It was postulated that with D. variabilis overwintering is a requirement for release of questing behaviour (Wilkinson, 1968).

Carbon dioxide as a stimulant and an attractant for certain blood-sucking arthropods is well documented in the literature (Reeves, 1951, 1953 and Brown, 1951). Garcia (1962) observed that quiescent ticks, Ornithodoros coriaceus Koch, were activated by expired human breath. Subsequently laboratory experiments showed that carbon dioxide was an important activating agent. Smith, et al. (1946) reported an increase in D. variabilis density along road side and animal trails and attributed this behaviour to the CO_2 gradient from automobile traffic and passing animals. McEnroe (1971) found similar results in a different study area. Glasgow and Collins (1948) reported that this tendency was so prominent on Long Island that for some heavily infested regions, as much as 90% of the tick population was concentrated in less than 10% of the area.

IV. ECOLOGY OF TICKS

A. Seasonal Fluctuation

D. variabilis live in a seasonal environment with seasonal fluctuations of biotic and abiotic conditions that affect the tick populations. Seasonal periodicity has thus been observed in these ticks and the cyclic changes are thought to be primarily due to effects of temperature, humidity, the availability of suitable hosts and vegetation cover. Hall and McKiel (1961) reported that in Nova Scotia ticks appeared in early April and by the beginning of July the numbers had decreased sharply. Bishopp and Smith (1938) in Maryland, found that ticks appear from mid-March to mid-April, declining sharply after mid-July. At Martha's Vineyard in Massachusetts adult ticks were reported to be active from April to the end of August (Smith and Cole, 1941). Garvie, et al. (1978) observed in western Nova Scotia, bimodal larval activity from April to September with a peak activity (3.95 larvae per host) in June and another in August. Nymphal activity was unimodal with a peak (3.85 nymphs per host) in June. Adult tick activity was from April to mid-August with one peak in May or June.

In Massachusetts, D. variabilis was observed to stop feeding in autumn though the temperatures were higher than those prevailing in spring (Atwood and Sonenshine, 1967).

This is attributed to the influence of photoperiod on the initiation of diapause. The questing ticks make up the potential breeding population. Therefore the sum of seasonal questing activity plays a major role in the regulation of population size (Smith, *et al*. 1946).

B. Soil Microclimate

Conditions within the soil microclimate regulate the initiation of activity and the ambient water stress condition regulates the termination of activity. Both these factors combine to regulate activity by limiting tick survival (McEnroe, 1974). McEnroe (1974) found that seasonal peak activity periods had the following factors in common: (i) both soil and air temperatures remained above 20°C for a minimum of five hours, ii) soil level microclimate, due to rain and or heavy dew remained at or near saturation for at least two days, (iii) during this period of saturation the soil temperature ranged from 15°C to 25°C for more than 50% of the time, (iv) peak days all had air temperature of 22°C. Milne (1950) pointed out that temperature of the soil microclimate is more important in affecting tick behaviour than ambient temperature. Due to thermal capacity of the soil and insulating properties of the vegetation mat, the temperature at soil level below the vegetation mat is more stable than air temperature (Mackinney, 1929).

The soil level microclimate is also strongly influenced by the radiant heat exchange (Geiger, 1965). In effect, the soil temperature will follow the average change rather than daily fluctuations of ambient air temperatures. D. variabilis activity was reported with air temperature as low as 5°C (Hall and McKiel, 1961). The temperature of the soil level microclimate was probably higher.

During winter months a blanket of snow insulates the soil surface from ambient temperatures (Pruitt, 1970; Aitchison, 1974) such that the soil temperature remains near 0°C. Aitchison (1977) concluded that the soil surface habitat is a thermally stable environment throughout the year. Animals that live on the soil surface were studied by Kühnelt (1961), Kevan (1972) and Aitchison (1977) and invertebrates reported include Protozoa, Acoelomata, Pseudocoelomata, Annelida, Mollusca, Onychophora, Crustaceans, Myriopoda, Tardigrada, Arachnida and many insects. No ticks were reported in the studies of these authors. It has been suggested that dehydration of an insect prior to diapause facilitates its ability to survive cold temperatures (Payne, 1927). At temperatures below preferred range, stupor and immobility occur in many invertebrates.

C. Air Temperatures

Temperature is known to influence tick activity, which begins when temperatures reach approximately 5°C (Hall and McKiel, 1961). McEnroe (1974) reported that the indirect relationship of activity to air temperature was shown by the start of activity in April when the average maximum temperature was about the monthly normal of 11.5°C, and the absence of activity when the average maximum temperature was below 11.5°C. The average maximum temperature for the weeks immediately prior to activity was from 9°C to 13°C and for the first weeks of activity, from 11.5°C to 15.5°C. McEnroe (1974) concluded that short term periods of high temperature will not induce activity. He found that at Lincoln, Nebraska, days with a maximum temperature of 26°C did not induce activity. He concluded that air temperature has a slow cumulative effect on the initiation of activity.

MacLeod (1934) reported that the temperature at which development is most rapid in *I. ricinus* is not a fixed value irrespective of humidity, but that it varies with humidity. At 20°C the humidity at which development is most rapid is 85%, the rate decreasing at temperatures above and below. These two factors operate simultaneously as variables in nature and therefore must be considered together.

Smith, et al. (1946) and Atwood and Sonenshine (1967) found no significant correlation between air temperature and the number of active ticks and therefore rejected air temperature as a factor affecting tick activity. Tick activity ceases in the fall when temperatures are much higher than at the start of activity in the spring.

Atwood and Sonenshine (1967) found significant correlation between daily numbers of larvae and nymphs, and solar energy, measured in langleys. Their data suggested that larval attachment in the fall ends when total solar energy falls below 200 langleys. The mean for the first two days of spring larval activity was 204 langleys.

Water uptake in ticks is affected by low winter temperatures. After winters with mean temperatures below 0°C the size of the adult cohort (McEnroe, 1975a, b) was at a minimum and following winters with a mean above 0°C the adult cohort increased. This increase is due to decreased winter mortality. Ticks can survive temperatures as low as -20°C for short periods (Smith, et al. 1946). At 0°C and below, tick survive only under saturated moisture conditions. The efficiency of their water pump rapidly drops with decreasing temperatures (McEnroe, 1971). Wallwork (1960) maintained that seasonal changes in temperature in North America stimulated movement of mites from litter to the humus as autumn progressed and the process was reversed as spring arrived. Ticks might also be affected in the same way.

D. Light

Bennett (1974) recognized a strong photonegative response in engorged _B_. _microplus_. This suggested that light might influence the pattern of oviposition. Experiments showed that ticks held at a steady temperature in darkness oviposited marginally better than ticks held under diurnal temperatures and light circles. He concluded that light had no significant effect on the oviposition of _B_. _microplus_.

Atwood and Sonenshine (1967) reported a relationship between the number of adult ticks active each day and the amount of daily solar radiation received. On overcast days numbers of adult ticks collected were low. Data did not show that solar energy is the triggering mechanism for initiation and termination of seasonal activity.

E. Humidity

Temperature and humidity are integrally involved in the survival, development and activity of D. variabilis populations. Several studies on the effect of humidity on a variety of tick species indicate that humidity by itself is not directly related to their rhythm of activity (Milne, 1945). He reported that autumn peaks of I. ricinus were invariably less than the spring peaks and yet humidity was higher in autumn than in spring.

Humidity falls to its lowest point during the heat of the day and rises during the cool of the night but at this time, much less tick activity occurs. Dodds, et al. (1969) stated that the presence of considerable moisture as noted by Bishopp and Smith (1938) is necessary to maintain high tick populations. In most tick species humidity affects development. Oviposition is hampered without humidity and development of larvae and nymphs is also affected. In D. variabilis the optimum humidity for oviposition is 85%. Bennett (1974) evaluated effects of humidity by suspending ticks over super-saturated salt solutions (humidity $>$ 85%), silica gel (humidity = 29%) and $CaCl_2$ (humidity $<$ 10%), and measuring egg production. He found that B. microplus laid more eggs at humidities of 85% and above. He also found that eggs laid at 45% to 100% relative humidity had a higher hatch rate than those laid at lower humidities. Hitchcock (1955) also reported that extreme dryness impaired both efficiency of oviposition and viability of the eggs in *B. microplus*.

F. Vegetation

Areas covered with grass or underbush (Bishopp and Smith, 1938; Sonenshine, *et al*. 1966) are known to harbour large numbers of *D. variabilis*. Woodland trails and grass centres of old logging roads are also infested with ticks (Sonenshine, *et al*. 1966). Ticks occur less frequently in forests (Bishopp and Smith, 1938). A sedge area (Dodds, *et al*. 1969) had high infestation rates, as well as vegetation adjacent to animal paths, man-made roads and trails used by animals. Hall and McKiel (1961) collected a large number of adult *D. variabilis* from the grass and raspberry (*Rubus* sp.) reaching 38-51 cm above ground level. They also reported a variety of other habitats that supported *D. variabilis*, e.g., wet riverside meadows, cutover access in spruce forests, and sweet fern barrows.

G. Tick Distribution on Body of Host

The majority of larvae, nymphs and adults attach to the ears of the host but a few are often found around the snout, eyes, head and shoulder region.

MATERIALS AND METHODS

I. STUDY AREA

Delta Marsh is approximately 120 km northwest of Winnipeg, Manitoba, on the south shore of Lake Manitoba (Fig. 2). The Marsh, approximately 15,000 hectares in area, is dominated by macrophytes such as Cattails (*Typha latifolia*), bulrushes (*Scurpus* spp.), and reed grass (*Phragmites communis*), and is separated from the lake by a long sand ridge covered with dense sandbar willow (*Salix interior*), peachleaf willow (*Salix amygdaloides*), green ash (*Fraxinus pennsylvanica*) and Manitoba maple (*Acer negundo*). The marshland has meadows, sloughs, wide bays and narrow channels. The study area lies within the aspen parkland (Bird, 1961). Within this area lies Oxbow Woods (Fig. 3). The dominant tree species in the wood lot include bur oak (*Quercus macrocarpa*), Manitoba maple (*A. negundo*) and green ash (*F. pennsylvanica*), and the shrub understory is composed of beaked hazelnut (*Corylus cornuta*), American hazelnut (*Corylus americana*) and wolfberry (*Symphoricarpus occidentalis*). The area has an annual precipitation of 387.0 mm and a mean annual temperature of 1.8°C. Summer temperatures may exceed 38.0°C and winter temperatures may exceed -38.0°C (Appendix V).

Figure 2. Map of the south shore of Lake Manitoba showing Delta Marsh and study area.

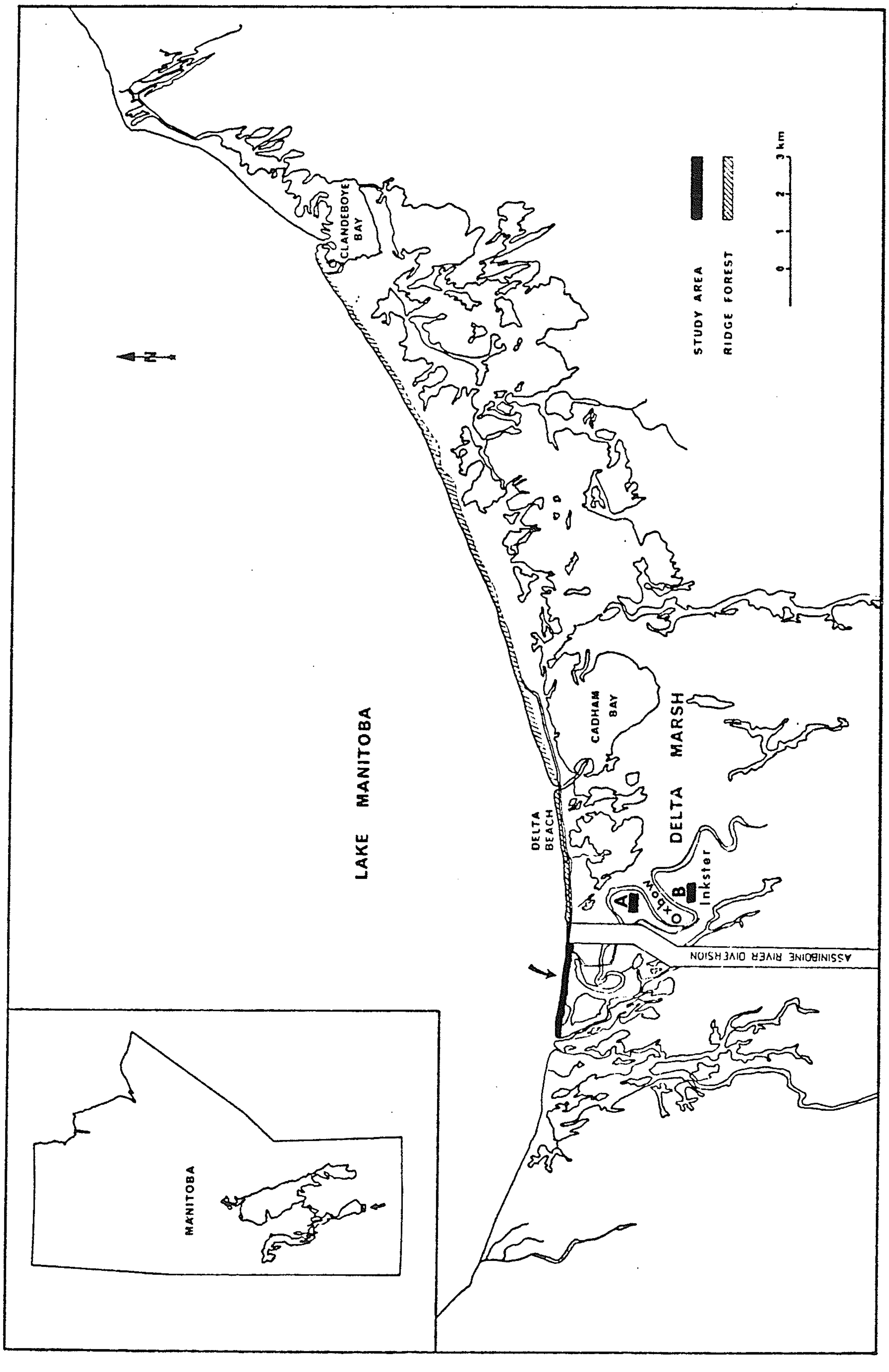
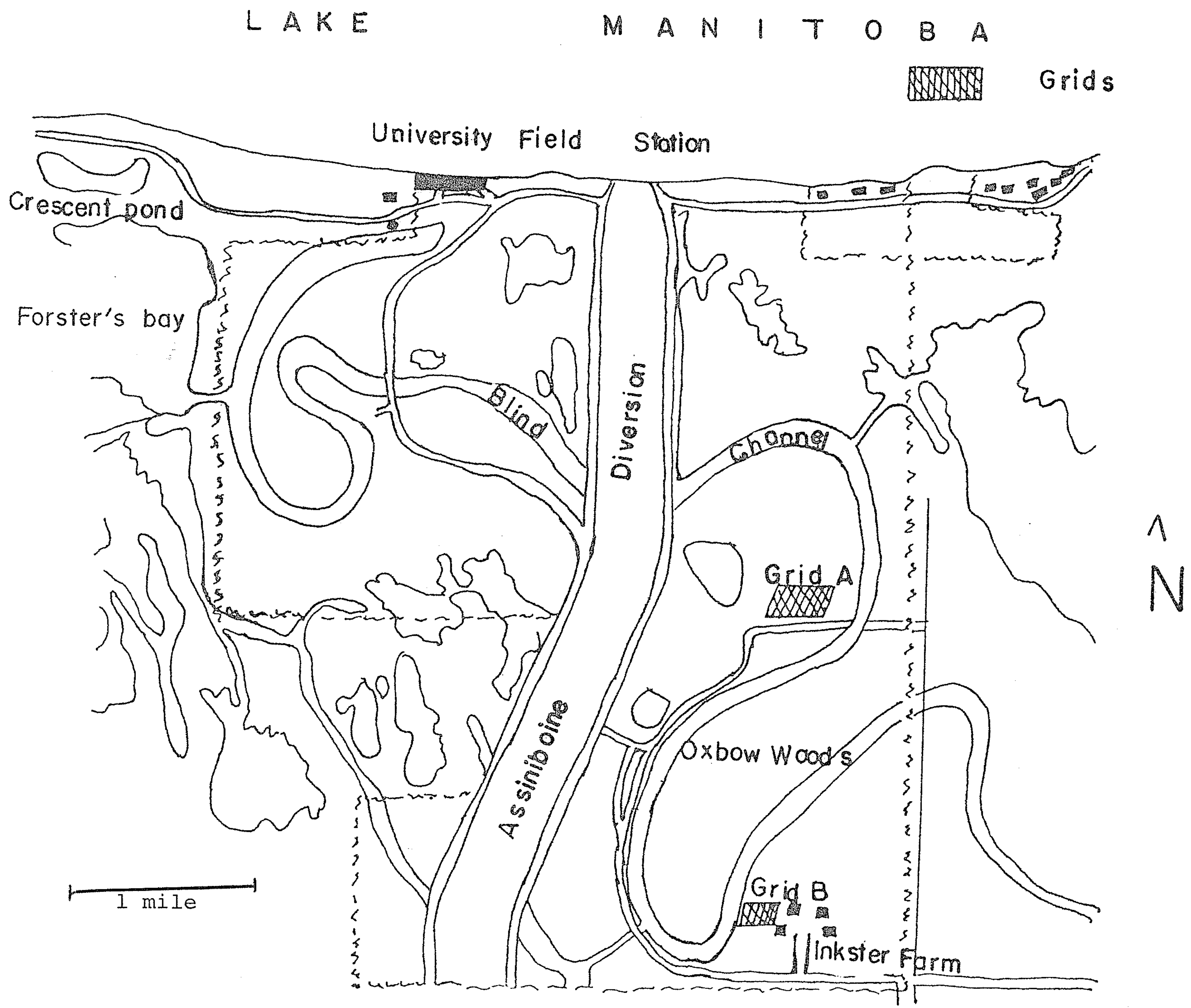

LAKE MANITOBA
CLANDEBOYE BAY
CADHAM BAY
DELTA BEACH
DELTA MARSH
A
B
Oxbow
Inkster
ASSINIBOINE RIVER DIVERSION
N
STUDY AREA
RIDGE FOREST
0
1
2
3 km
MANITOBA

Figure 3. Map of Delta Marsh showing Oxbow Woods (Grid A) and Inkster Farm (Grid B).


LAKE MANITOBA
Grids
University Field Station
Crescent pond
Forster's bay
Blind Channel
Diversion
Assiniboine
Grid A
Oxbow Woods
Grid B
Inkster Farm
N
1 mile

II. MAMMAL TRAPPING

Large numbers of mammals were examined during the summers of 1977 and 1978. Several methods were used for capturing animals.

A. Rodents

Two trapping Grids A and B (Fig. 3), each 90 x 70 metres were set up in Oxbow Woods and at Inkster Farm respectively. One third of Grid A was in the woods and the other two thirds was outside the woods in open grassland with tall grass, short grass and herbs and shrubs. Grid B was in the woods on the edge of farmland. The two grids were separated by a wooded area and by a Blind Channel (Fig. 3). Each grid contained eighty points, 10 m apart, marked with a 1 m long lath to which an orange tape was attached. Sherman traps were numbered and placed in the vicinity of each post. Traps were set on three consecutive nights at two-week intervals, and baited with a mixture of peanut butter and rolled oats (2:1 by volume). Cotton batting was added to provide protection from cold and wet nights. Rodents caught in the traps were collected the following morning between 0800 and 0900 hours, transported to the laboratory, anaesthetized with ether and examined under a dissection microscope for the presence of ticks. Ticks were removed and placed in labelled vials in 70% ethanol for later identification.

Each rodent was toe-clipped according to a predetermined pattern (Jenkins, 1948) to permit future identification of individuals. Rodents were returned at 1500 hours to the specific areas in which they were caught.

Rodent populations were defined in terms of trap nights and rodent densities. Trap nights are the product of the number of traps on the grid and the number of nights of trapping. Rodent densities were calculated in two ways: (i) the number of rodents per trap night, and (ii) the number of rodents per hectare.

B. Large Mammals

Live-trapping of larger mammals (weasels, raccoons, etc.) was done with wire cage traps of different sizes. Animals were taken to the laboratory and immobilized by injecting three to four millilitres (10 mg/cc solution) of phencyclidine hydrochloride (Sernylan:Bio-ceutic Laboratories, Inc., St. Joseph, Missouri). Weasels and squirrels were examined for ticks under a dissecting microscope. A hand lens was used for larger mammals. Ticks were removed and stored in 70% ethanol. Animals were ear-tagged for easy identification, and then returned to capture sites upon recovery. See Appendix VI" for notations recorded."

C. Road Kills and Other

Mammals were also retrieved from road kills and from other projects conducted by research students at Delta Marsh. Ticks found crawling on humans were removed and stored in 70% ethanol. Sex and stage of development of each tick were recorded for all ticks collected.

Prevalence, i.e., number of hosts infested/total number of hosts examined, expressed as a percentage, was used to define level of host infestation. Intensity, i.e., mean number of ticks per infested host $\frac{(\text{Total number of all ticks})}{(\text{Total number of infested hosts})}$ was used to express tick densities on hosts, and occurrence, i.e., Intensity x Prevalence, was used as a measure of parasitism.

III. BIRDS: MIST NETTING

In the first year of this study birds were obtained from an Ornithology research group which operated several mist nets along the Delta Beach Ridge. In addition, a number of ground birds were trapped in wire cages used for trapping squirrels. A few birds were shot with a 410 shotgun by a parasitology research team. In the second year of the study, nylon mist nets, mesh 1 1/2, height 2 m, length 12.5 m and shelf 5 were operated in Oxbow Woods and along the ridge (Fig. 3). The following features were recorded; number of nets operated and period of operation (essential for determining net hours and bird densities). Bird species, age, sex, wing size, band number and date were also recorded. All birds caught in nets were examined for ticks under a dissecting microscope. Ticks were removed and stored in 70% ethyl alcohol. Only a few birds were banded; namely, northern oriole (*Icterus galbula*) and gray catbird (*Dumetella carolinensis*):band size A; least flycatcher (*Empidonax minimus*), yellow warbler (*Dendroica petechia*), house wren (*Troglodytes aedon*) and clay-coloured sparrow (*Spizella pallida*):band size 0.

Bird densities were calculated according to net hours. Net hours = Number of nets x hours of netting, e.g., 5 nets up @ 8:00 a.m. to 11:00 a.m. = 15 net hours. Therefore

$$\text{Bird density} = \frac{\text{Number of birds caught}}{\text{Net hours}}.$$

Bird nomenclature follows the A.O.U. check-list of N. Amer. Birds (1957) and the 32nd Supplement (1973).

IV. BIRD NESTS

A dozen nests were examined for ticks; 3 western kingbird (*Tyrannus verticalis*), 1 eastern kingbird (*Tyrannus tyrannus*), 2 barn swallow (*Hirudo rustica*), 3 red-winged blackbird (*Agelaius phoeniceus*), and 3 yellow-headed blackbird (*Xanthocephalus xanthocephalus*). Nests were placed in Tullgren funnels and left exposed to heat from 100-watt white light bulbs for forty-eight hours. The spouts of the funnels were immersed in 70% ethanol. Ticks, if present, would migrate away from the heat source and be trapped in the ethanol.

V. VEGETATION

A. Vegetation Sampling

A grid was set up in each habitat and twenty 1/16 m^2 quadrats were selected in each, using a table of random numbers. This high number of small quadrats is effective in showing species variation (Phillips, 1959). Basal area (cover) and sociability as modified by Braun-Blanquet (1932) Appendix VII, and the number of species present in each plot, were recorded. Lists of species from each area were made (Scoggan , 1957).

For description of plant communities, the following quantitative measures were used:

$$\text{Frequency} = \frac{\text{number of quadrats of occurrence}}{\text{total number of quadrats sampled}} \times 100$$

Dominance = Percent cover of each species per quadrat

$$\text{Importance Value (IV)} = \text{Relative Density} + \text{Relative Frequency} + \text{Relative Dominance}$$

$$\text{Relative Density} = \frac{\text{Number of individuals of a species}}{\text{Total number of individuals of all species}} \times 100$$

$$\text{Relative Frequency} = \frac{\text{Frequency of species}}{\text{Sum of Frequency Values of all species}} \times 100$$

$$\text{Relative Dominance} = \frac{\text{Total basal area (cover) of one species}}{\text{Total basal area of all species}} \times 100$$

(For Scales of Cover and Sociability see Appendix VII).

$$\text{Jaccard's Index of Similarity} = \frac{\text{number of common species}}{\text{no. of sp. unique to a} + \text{no. of sp. unique to b} + \text{no. of common species (c)}} \times 100$$

where c is the common number of species; a is the number of species unique to the first community and b is the number unique to the second.

B. Tick Flagging

To determine densities of adult ticks on vegetation, a 1 x 1 m white terry cloth was fixed to a 1 m long rod and dragged (Fig. 4) at a reasonably constant rate, at different times of the day, over the following habitats: (i) low grass,

Figure 4. Photograph showing dragging procedure.

(ii) tall grass, (iii) mixed herbs and shrubs. Four drags of 25 m length were made over a 100 square metre area in each habitat. $\bar{x}$: SE of ticks were calculated for each habitat. Adult tick densities = $\frac{\text{number of ticks from dragging}}{\text{area of dragging}}$ and was expressed as x ticks were square metre. The following environmental data were recorded: temperature; humidity; light intensity at 1/4 m, 1/2 m, 1 m and 2 m; time of day and H_20 content of organic litter. Organic samples were taken from each habitat in sealed plastic bags, transported to the laboratory and weighed to the nearest gm. Samples were then placed in an oven at 105°C for 24 hours. Weights were taken, samples dried for another 24 hours and weighed again. This procedure continued until weights remained constant.

VI. WINTER INVERTEBRATE TRAPPING

Twenty sites with high tick populations were selected in the five habitats during periods of high tick activity. In late fall, a few days before the first snow fall, simple pitfall traps (Appendix VIII), modified from those of Näsmack as described and modified by Aitchison (1974), were set in the five habitats in the study area. Each trap consisted of a plastic cup filled with a mixture (1:3) of water and ethylene glycol (a non-repellent preservative which does not freeze at -30^{o}C). The cup was placed in a larger cup whose rim was level with the surface of the soil. A wooden cover was placed over the plastic cups to prevent snow from filling the inner cup. A wire handle was fixed to two diagonal corners of the wooden cover and to the top of a 1 m long lath with an orange tape, which also helped to mark the position of the trap. Traps were then left for four and half months (from the 1st week of November, 1978 until the third week of March, 1979.

Traps were removed a short while before the snow started to melt. Invertebrates trapped in the ethylene glycol were removed, stored in jars and taken to the laboratory for identification. Samples of organic litter in the vicinity of the traps were also collected in sealed plastic bags, and by means of Tullgren funnels, any invertebrates present were collected in 70% ethanol and identified.

VII. LIFE CYCLE

In 1977 adult ticks collected by flagging were placed in vials stoppered with cotton wool, and placed in the refrigerator at 4°C until November, 1977 when they were fed on rats. Ticks were checked every 8 hours to see if they were attached and were engorging. In 1978, six rats and two rabbits were used to feed 72 adult ticks freshly collected from the field. Four male and four female ticks were placed on each rat and six male and six females on each rabbit. One rat had only female tick feeding. Engorged ticks were removed and placed in vials plugged with cotton wool and placed in an environmental chamber with relative humidity of 85% and temperature of 27°C. The chamber had a 14 hour day and a 10 hour night cycle. Date of placing engorged ticks in chamber, date first eggs were laid and date of hatching were recorded. Some of the egg clutches were removed and stored in the deep freeze for a later egg count.

RESULTS

I. TICK SPECIES AT DELTA MARSH

Three species of ticks were found at Delta Marsh, i.e., *Dermacentor variabilis* (Say), *Haemaphysalis leporispalustris* (Packard), and *Haemaphysalis chordeilis* (Packard). Species were identified to genera by Key to Family and Genera (Gregson, 1956) and Key to Families, Genera and Selected Species of Metastigmata-Adults, in Manual of Medical Entomology (Furman and Catts, 1970) (Appendix IX). Taxonomy and nomenclature appear in Appendix X.

II. HOST POPULATIONS OF MAMMALS

Twenty-two species of mammals (Table 1) represented by 1690 specimens were examined for ticks. Twelve species comprising 1580 specimens were infested (Table 2). Four species of mice and voles, a total of 1494 specimens, were taken on Grid A and Grid B. One species of shrew (83) and one of chipmunk (13) were taken from Grid A and Grid B, respectively. Eleven franklin ground squirrels were captured on Grid A in 1977, and 24 in 1978 and the remaining species of squirrels (19 specimens) were captured elsewhere.

Table 1. Mammalian Hosts Caught in Traps in 1977 and 1978

Host/Authority	1977	1978	Total
Clethrionomys gapperi (Vigors)	189	526	715
Microtus pennsylvanicus (Ord)	121	110	231
Peromyscus maniculatus (Wagner)	120	375	495
Zapus hudsonius (Zimmermann)	38	115	153
Rattus norvegicus (Berkenhout)	2	0	2
Mus musculus Linneaus	1	0	1
Lepus americanus Erxleben	1	4	5
Lepus townsendii Bachman	1	0	1
Sylvilagus floridanus (J.A. Allen)	1	0	1
Tamiasciurus hudsonicus (Erxleben)	9	4	13
Spermophilus richardsonii (Sabine)	0	1	1
Spermophilus franklinii (Sabine)	11	45	56
Spermophilus tridecemlineatus (Mitchell)	1	1	2
Sciurus carolinensis Gmelin	-	3	3
Sorex cinereus Kerr	36	47	83
Eutamius minimus Bachman	-	13	13
Lasuirus borealis (Müller)	1	-	1
Odocoileus virginianus (Zimmermann)	1	-	1
Mephitis mephitis (Schreber)	1	1	2
Procyon lotor (Linnaeus)	1	1	2

cont'd

Table 1 cont'd. Mammalian Hosts Caught in Traps in 1977 and 1978

Host/Authority	1977	1978	Total
Mustela erminea Linnaeus	4	2	6
Mustela frenata Lichtenstein	1	2	3
Total	540	1150	1690

Table 2. Hosts Infested With *D. variabilis* Ticks, 1977 and 1978.

Hosts		1977					1978				
		No. of Hosts Examined	Hosts Infested	Tick Infestation Larvae	Nymphs	Adults	No. of Hosts Examined	Host Infested	Tick Infestation Larvae	Nymphs	Adults
Clethrionomys gapperi	♀	72	18	11	29	-	220	38	86	86	-
	♂	59	28	18	91	-	122	40	958	141	-
	J	58	13	6	13	-	184	31	172	67	-
Microtus pennsylvanicus	♀	38	14	15	35	-	33	24	19	88	-
	♂	65	24	59	75	-	35	24	28	104	-
	J	18	10	2	10	-	42	13	8	21	-
Peromyscus maniculatus	♀	21	2	4	-	-	75	5	6	8	-
	♂	65	14	61	16	-	191	15	181	7	-
	J	34	4	3	5	-	109	1	2	-	-
Zapus hudsonius	♀	26	5	8	7	-	41	9	3	7	-
	♂	8	-	-	-	-	47	12	11	5	-
	J	4	2	-	1	-	27	7	13	2	-
Tamiasciurus hudsonicus	♀	5	-	-	-	-	2	-	-	-	-
	♂	4	2	-	-	2	2	-	-	-	-
Spermophilus franklinii	♀	1	1	-	-	1	13	6	-	-	10
	♂	10	2	-	-	2	32	12	-	-	19
Sciurus carolinensis	♀	-	-	-	-	-	2	1	-	-	4
	♂	-	-	-	-	-	1	1	-	-	3

cont'd

Table 2 cont'd. Hosts Infested With *D. variabilis* Ticks, 1977 and 1978.

		1977					1978				
		No. of Hosts Examined	Hosts Infested	Tick Infestation Larvae	Nymphs	Adults	No. Hosts Examined	Host Infested	Tick Infestation Larvae	Nymphs	Adults
Odocoileus virginianus	♀	1	1	-	-	1	-	-	-	-	-
	♂	-	-	-	-	-	-	-	-	-	-
Mephitis mephitis	♀	1	1	-	-	25	1	1	-	-	38
	♂										
Procyon lotor	♀	-	-	-	-	-	1	1	-	-	17
	♂	1	-	-	-	-	-	-	-	-	-
Mustela erminea	♀	3	1	-	-	1	1	1	-	-	1
	♂	1	-	-	-	-	1	1	-	-	3
Mustela frenata	♀	1	1	-	-	1	1	1	-	-	1
	♂	-	-	-	-	-	1	1	-	-	1
Total		496	143	187	282	33	1084	245	1487	536	97

The four mice and voles in the study were *Clethrionomys gapperi* (Vigors), *Microtus pennsylvanicus* (Ord.), *Peromyscus maniculatus* (Wagner) and *Zapus hudsonius* (Zimmerman). No taxonomic measurements were made in order to identify subspecies but an examination of the map of subspecies distribution in Banfield (1974) revealed that the following subspecies were probably involved in this work; *C. gapperi loringi* (V. Bailey), *M. pennsylvanicus drummondii* (Audubon and Bachman), *P. maniculatus bairdi* (Hoy and Kennicott) and *Z. hudsonius hudsonius* (Zimmermann).

C. gapperi, *M. pennsylvanicus*, *P. maniculatus* and *Z. hudsonius* were regularly live-trapped on the grids and *C. gapperi* (715) was the most dominant numerically, followed by *P. maniculatus* (395), *M. pennsylvanicus* (231) and *Z. hudsonius* (153). Mortality in traps was less than 5% for larger mammals and small rodents, but 100% for *Sorex cinereus*.

In the following discussion, shrews and chipmunks are not included as no ticks were found on them. Figure 5 and Figure 6 show positions of traps and rodent dispersion in Grid A and Grid B respectively. Figure 5 shows the concentration of *C. gapperi* and *P. maniculatus* in the wooded area on Grid A while *M. pennsylvanicus* and *Z. hudsonius* are in the grassy section of the grid. Dispersion of all mice on this grid appeared to be non-random, reflecting a degree of aggregation which appeared to be associated with ground cover.

Figure 5. Grid A showing trap-lines and host distribution.

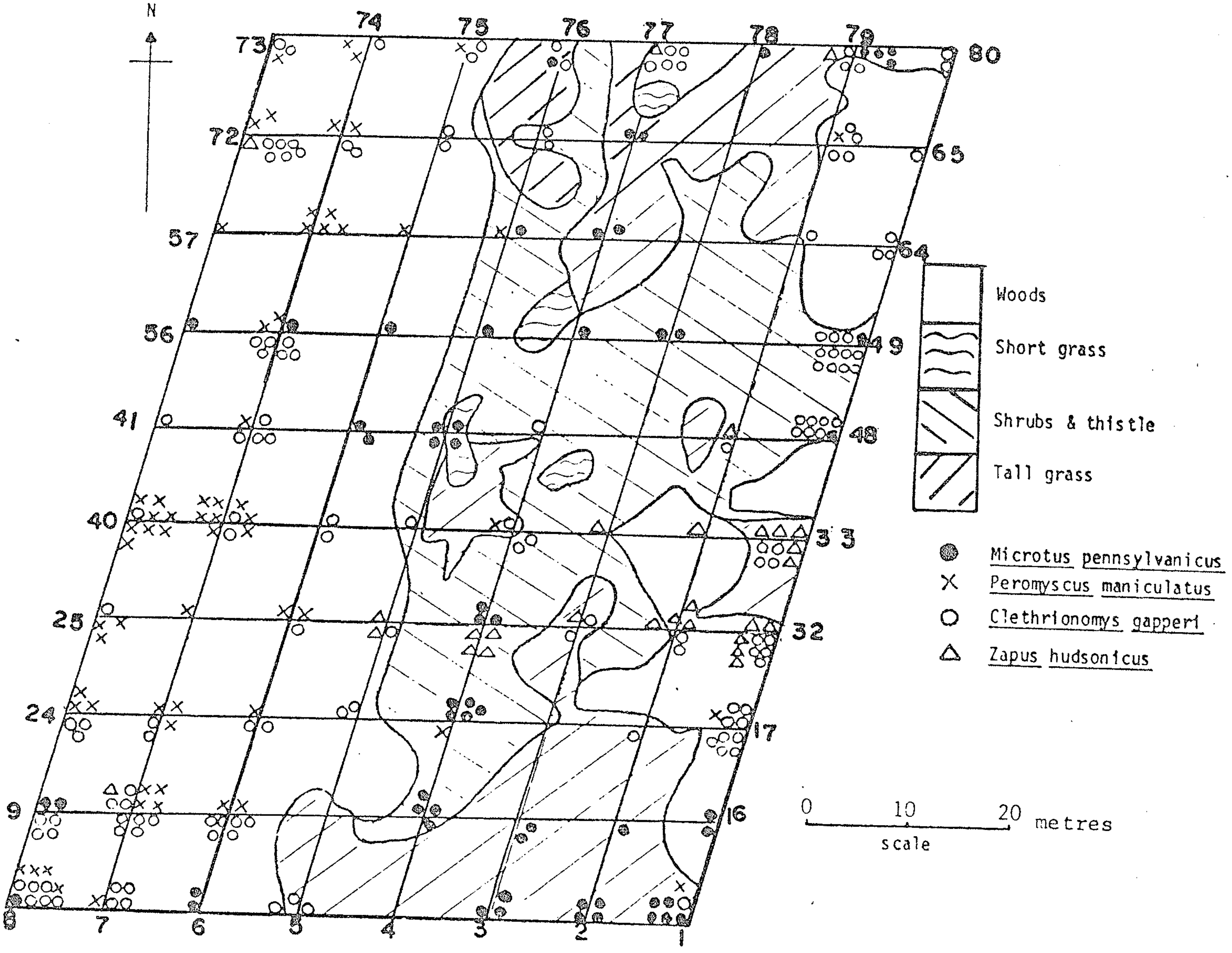
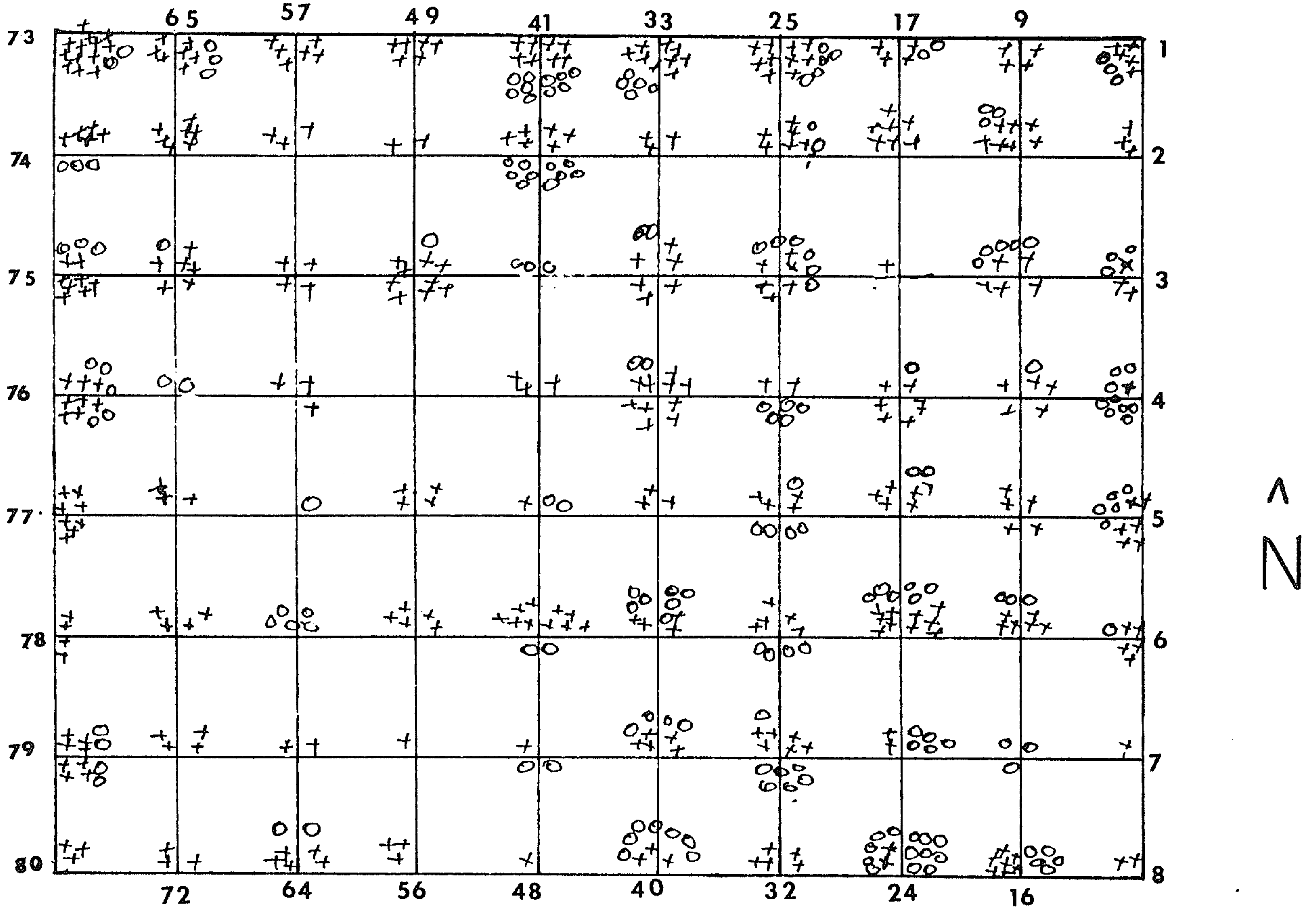

N
73
74
75
76
77
78
79
80
72
65
57
64
56
49
41
48
40
33
25
32
24
17
9
16
8
7
6
5
4
3
2
1
Woods
Short grass
Shrubs & thistle
Tall grass
Microtus pennsylvanicus
Peromyscus maniculatus
Clethrionomys gapperi
Zapus hudsonicus
0
10
20
metres
scale

Figure 6. Grid B showing trap-lines and host distribution.

+ = *Clethrionomys gapperi*
O = *Peromyscus maniculatus*



Dispersion of C. gapperi and P. maniculatus was uniform (Fig. 6) in Grid B, which was entirely in the woods. Both species were caught in high numbers and were more frequently caught in the same traps and showed a degree of trap addiction. Trapping results indicate that the two species co-exist and that apparently little interspecific competition occurs. Thirteen M. pennsylvanicus and three Z. hudsonius were caught in Grid B in contrast to 342 C. gapperi and 193 P. maniculatus. Z. hudsonius and M. pennsylvanicus seem to prefer open habitat over wooded habitat.

(A) Densities of Mammal Hosts

The trapping programme in this study does not permit absolute estimations of total populations of hosts by any of Mark and Recapture methods (Randolph, 1975a) because of trap addiction of the rodents. As the trapping effort remained constant throughout, it is justifiable to conclude that the numbers of rodents caught will indicate the relative seasonal variations in the rodent population densities.

Eighty Sherman traps set for 21 nights on Grid A in 1977 gave a total of 1680 trap nights, over an area of 0.6 hectare and caught 468 small rodents. Rodent density was 0.28 rodents per trap night or 780 rodents per hectare. In 1978, the same number of traps were set for 24 nights (1920 trap nights) and 475 rodents caught, giving a density of 0.25 rodents per trap night, or

791 rodents per hectare. These estimates of population densities are close for the two years on this grid and reflect high populations. Five hundred and fifty one rodents were caught in 18 trap nights on Grid B indicating a density of 0.4 rodents per trap night or 918 rodents per hectare. The population was much higher on Grid B than on Grid A.

Attempts to estimate accurately population size were made by applying the Lincoln or Peterson Index (Poole, 1974) (Appendix XI). Population estimates for Grid A for 1977 and 1978 are 257 and 18 small rodents respectively, with variances of 11243.2 and 7.1 and standard deviation 106.0 and 2.7. For Grid B, results for population estimation are 28.3 with $S^2 = 2784.4$, SD = 52.8. These results were not convincing and it seemed impossible to describe variability as computation of the variance was biased, and therefore only an approximation of variance of the true population. With small samples and small numbers of recaptures the bias of the estimate proved to be relatively large.

Further analyses of data were carried out using the Improved Stochastic Multiple-Recapture method by jolly (1965) (Appendix XII). This method proved more satisfactory as it allowed for both immigration and death. For purposes of population density estimates, numbers of rodents on Grid A in 1977 were low at the beginning of trapping on June 6.

As trapping continued, rodent numbers rose sharply and by July 5, a total 235 rodents had been present in the population. There was a drop in the population density and by August 31st, there were 32 rodents in the population. Figure 7(a) shows similar decline at the end of trapping.

In 1978 Grid A had a population of 25 rodents when trapping began on May 17th. Numbers increased steadily with a mean density increase of 0.8 ± 0.3 (SE) per fortnight and reached a peak density of 85 rodents by August 7th. There was a slight decline and by August 21st, population density had dropped to 76 rodents. Population density on Grid B was higher than on Grid A for both 1977 and 1978. This grid had a population of 31 rodents when trapping began on June 14th. A rapid phase of population growth began in July reaching a peak of 104 rodents by August 13th. A slight decline occurred by August 21st and there were 92 rodents in the population. Trapping data (Fig. 7c) support these results.

(B) Seasonal Dynamics of Host Populations

Seasonal occurrence of the major host species caught each trap night are given in Figures 8, 9 and 10. Mean fortnight catches are shown in Figure 7. These data include all rodents caught both for the first and second recapture.

Figure 7. Mean number of hosts caught per trapping period in each fortnight.

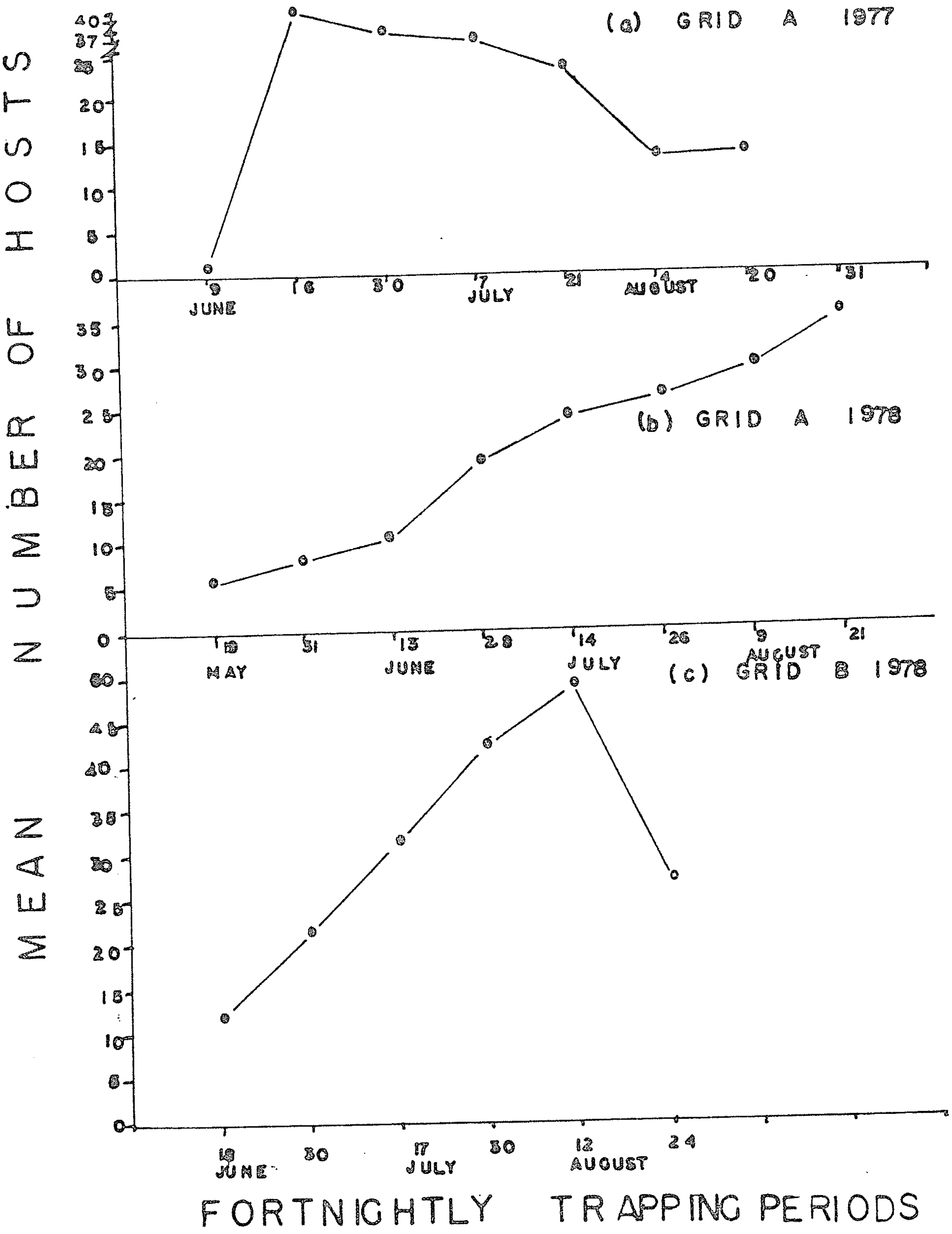

MEAN NUMBER OF HOSTS
(a) GRID A 1977
40
37
25
20
15
10
5
0
9 JUNE
16
30
7 JULY
21
4 AUGUST
20
31
(b) GRID A 1978
35
30
25
20
15
10
5
0
19 MAY
31
13 JUNE
28
14 JULY
26
9 AUGUST
21
(c) GRID B 1978
50
45
40
35
30
25
20
15
10
5
0
18 JUNE
30
17 JULY
30
12 AUGUST
24
FORTNIGHTLY TRAPPING PERIODS

Figure 8. Population densities of rodents on Grid A, 1977.

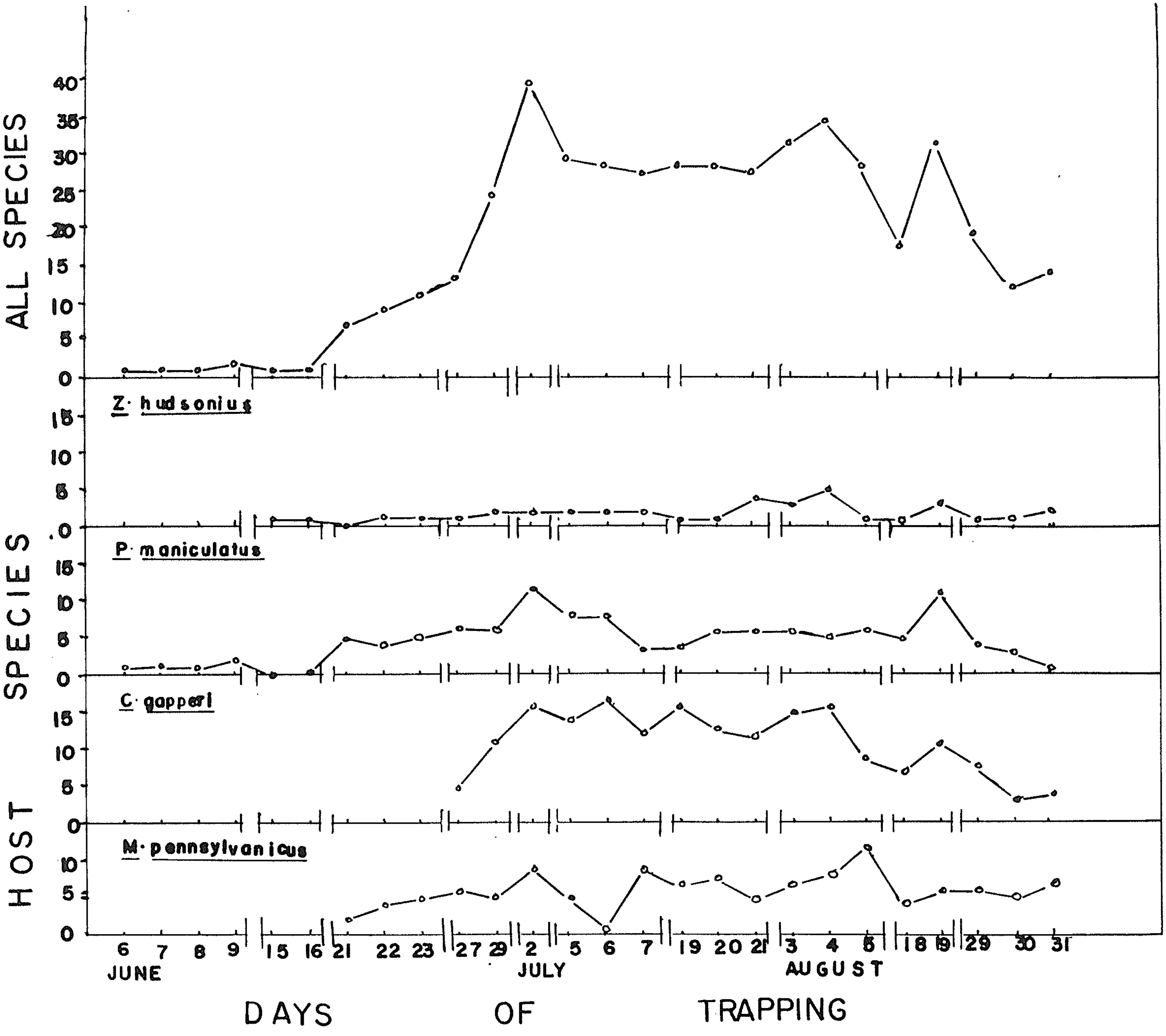
ALL SPECIES
SPECIES
HOST
40
35
30
25
20
15
10
5
0
Z. hudsonius
P. maniculatus
C. gapperi
M. pennsylvanicus
6
7
8
9
15
16
21
22
23
27
29
2
5
6
7
19
20
21
3
4
5
18
19
29
30
31
JUNE
JULY
AUGUST
DAYS OF TRAPPING

Figure 9. Population densities of rodents on Grid A, 1978.

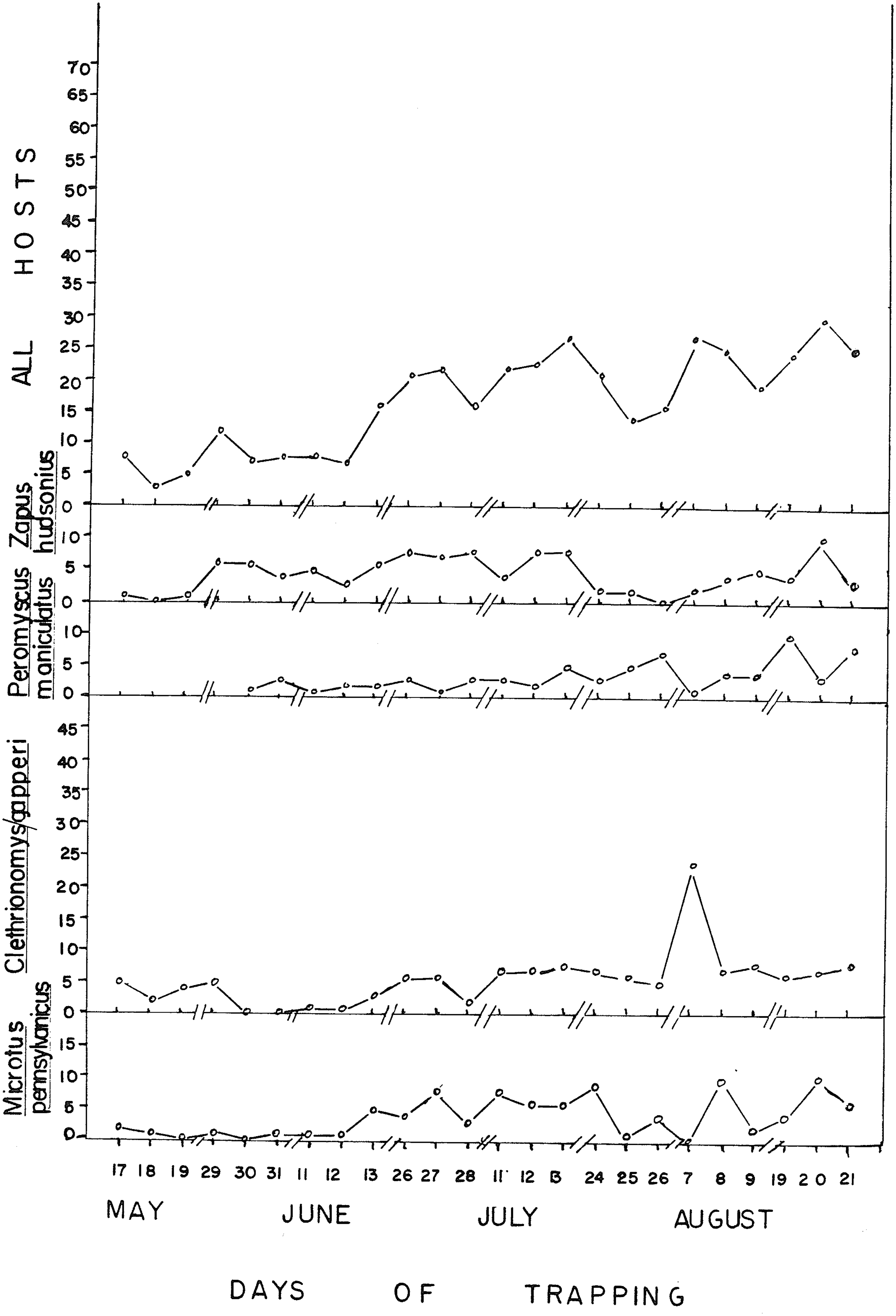
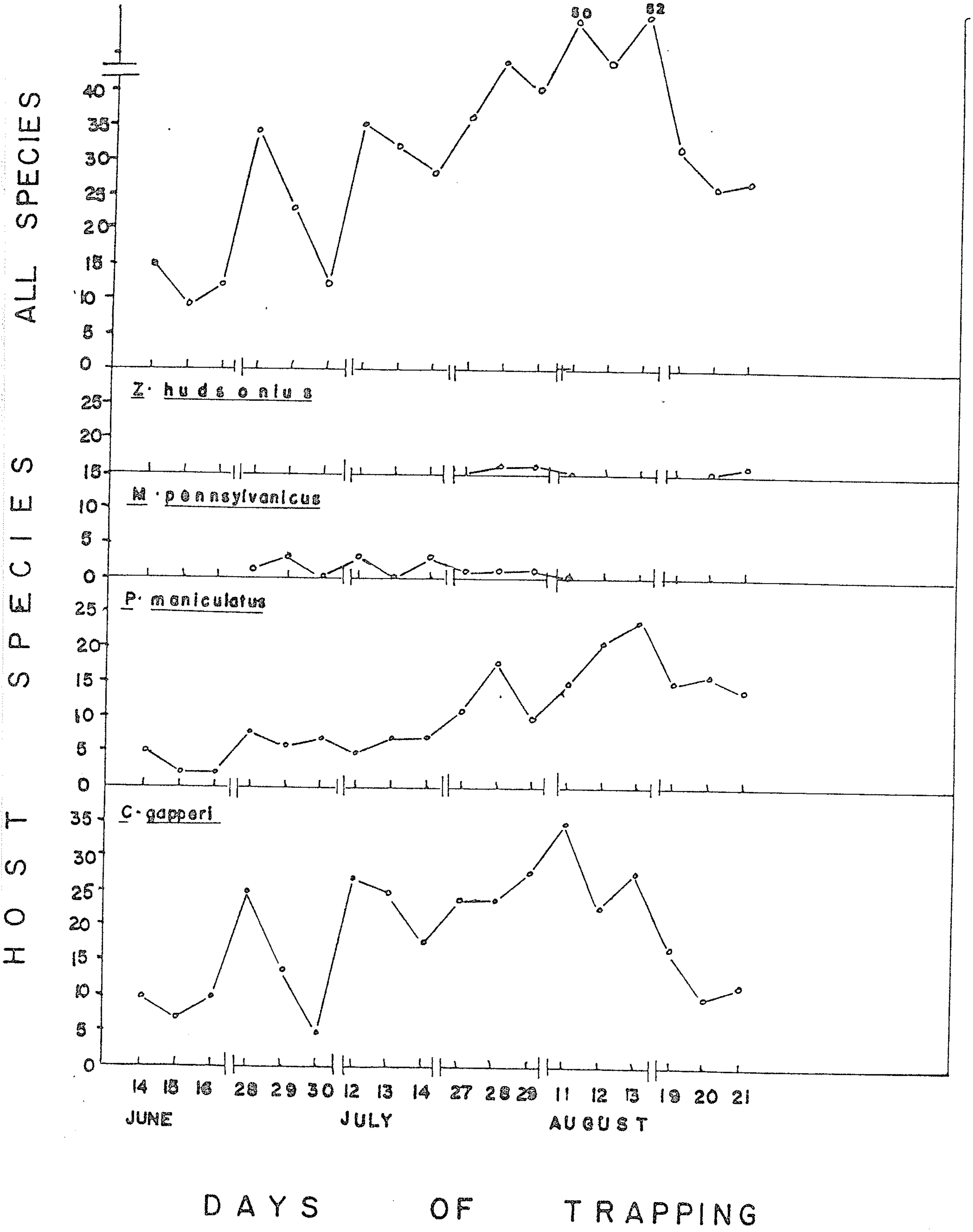

ALL HOSTS
70
65
60
55
50
45
40
35
30
25
20
15
10
5
0
Zapus hudsonius
10
5
0
Peromyscus maniculatus
10
5
0
Clethrionomys/gapperi
45
40
35
30
25
20
15
10
5
0
Microtus pennsylvanicus
15
10
5
0
17 18 19 29 30 31 11 12 13 26 27 28 11 12 13 24 25 26 7 8 9 19 20 21
MAY
JUNE
JULY
AUGUST
DAYS OF TRAPPING

Figure 10. Population densities of rodents on Grid B, 1978.


ALL SPECIES
HOST SPECIES
50
52
40
35
30
25
20
15
10
5
0
Z. hudsonius
M. pennsylvanicus
P. maniculatus
C. gapperi
14 15 16 28 29 30 12 13 14 27 28 29 11 12 13 19 20 21
JUNE
JULY
AUGUST
DAYS OF TRAPPING

Frequency distributions of hosts caught for the first time and recaptures appear in Fig. 11(a), (b) and (c). These frequency distributions show a gradual growth in population size. Growth appears normal in Fig. 11(a) and (b). Host numbers were low in May and June and were high in July and at the beginning of August. *C. gapperi*, *M. pennsylvanicus*, *P. maniculatus*, and *Z. hudsonius* showed a similar pattern of seasonal variation on Grid A in 1978, but *Z. hudsonius* were low in number in 1977 (Fig. 8 and 9). Seasonal distribution of hosts in Grid B, 1978, reveals similar distribution curves for *C. gapperi* and *P. maniculatus* (Fig. 10).

C. gapperi did not enter traps until the third week of June in 1977. *M. pennsylvanicus* and *Z. hudsonius* appeared in the second week of June. *P. maniculatus* were present from first day of trapping. All species showed a peak in July and August. Thirteen juveniles were caught in May and 20 in June. Many juveniles (52) entered the population in July and August and accounted for the sudden increase of the marked population (Table 3) towards the end of the trapping season. This suggests that breeding occurred in May and June. Numbers dropped towards the end of August (Fig. 8 and 10). This was probably due to such factors as death and emigration. Figure 9 shows a sudden reverse in numbers in August, which suggests an exponential growth in the host population. This may be due to late breeding of *C. gapperi* in 1978.

Figure 11. Rodent distributions on Grids A and B in 1977 (Grid A only) and 1978.

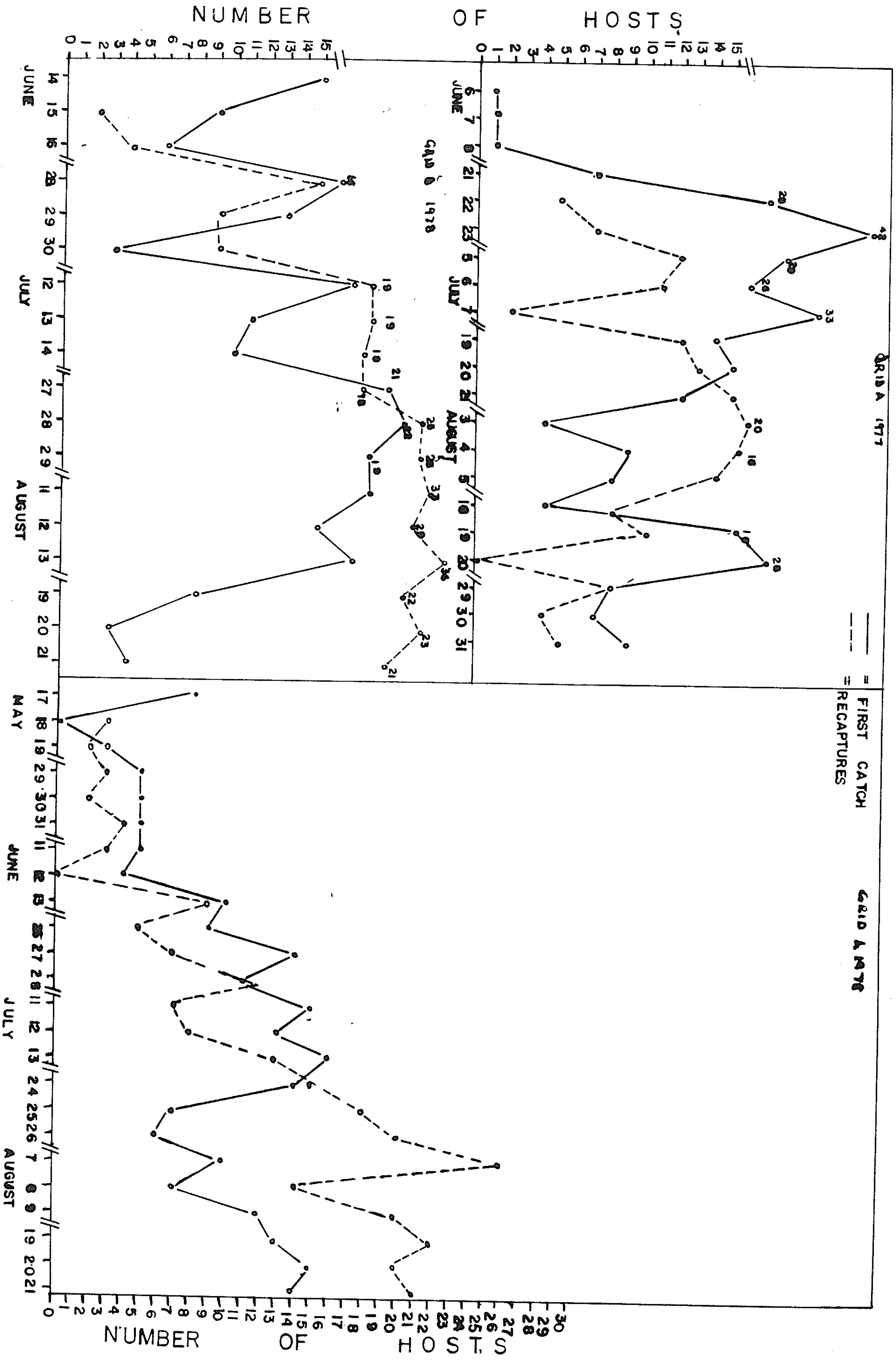

NUMBER OF HOSTS
GRID A 1977
GRID B 1978
GRID A 1978
—— = FIRST CATCH
– – – = RECAPTURES
JUNE
JULY
AUGUST
MAY
NUMBER OF HOSTS

Table 3. Number of Hosts Caught in Traps and Their Growth Stage

Year and Grid	Month	Juveniles	Adults	Males	Females	Total
1977 A	June	11	65	38	27	141
	July	58	148	85	63	354
	August	45	141	74	67	327
		114	354	197	157	822
1978 A	May	13	30	21	9	73
	June	20	70	42	28	160
	July	52	98	60	38	248
	August	88	101	60	41	290
		173	299	183	116	777
1978 B	June	32	77	21	56	186
	July	58	157	54	103	372
	August	100	131	37	94	362
		190	365	112	253	920
	Total	477	1018	492	526	2513

There were more male (197) than female (157) rodents on Grid A in 1977 (Table 3) and the ratio was ♀ : ♂1:1.3. In 1978 there were 183 male and 116 female rodents, ratio ♀ : ♂1:1.6. There were more females (253) than males on Grid B in 1978 with a ratio of ♀ : ♂ = 1:0.43. Test for differential trappability between males and females with a chi-square analysis of a 2 x 2 contingency table shows significant differences in trappability between males and females in the study area. The 1977 results gave an $X^2 = 0.63$ with 1df and a $P < 0.50$. With a 50:50 chance of males or females caught in traps, there is no apparent trend in differential trappability by sex. The difference between male and female is not inconsistent with the null hypothesis ($H_o : \delta = 0$). The population mean must be regarded to have equal frequency.

A preponderance of pregnant females over non-pregnant females occurred in June and July and this may account for growth of the populations in July and August in 1978 (Table 3). Growth in the population was assessed by the monthly increase in rodent numbers (Table 3). Mean weight and SE; Grid A, 1977 : 19.09 ± 0.3; Grid A, 1978 : 17.7 ± 0.3; Grid, 1978 : 18.3 ± 0.3. Data on Figure 12 show that the majority of rodents ranged between 16 and 20 grms. These figures are significantly different. Distribution is normal.

Maximum distances that voles travelled within the grids appeared greater for males than for females during the breeding season. This was possibly because more females were resident during the breeding season. One male was regularly caught in trap #8 at the beginning of the season but by the end of the season the vole had moved to trap #66 (Fig. 5) at the opposite end of the grid, a distance of 110 m. Ten male and 10 female C. gapperi, frequently recaptured, were randomly selected. Male and female voles were then paired according to weight. Bee-line measurements were made of the distances between traps where each vole was caught. Mean and standard deviation were calculated and paired t-test used to test the hypothesis that males travelled greater distances than females. Total distance travelled by C. gapperi males in sample was 901.5 m with $\bar{x}$: SD, 29.9 : 5.4 and for females total distance was 697 with $\bar{x}$: SD, 17.9 : 2.9. The t-test gave a $t > 1.65$ at 5% significance level. These results are significant and lead me to accept the hypothesis.

Data for trapped mice and voles from Grid A, 1978 are summarized below.

	% Female	% Male	♀ : ♂ Ratio
1978 May	30	70	1:0.43
June	40	60	1:0.67
July	39	61	1:0.63
August	31	69	1:0.45

(C) Diversity of Small Rodents

Diversity of the four major host species was calculated by the Simpson Index (Appendix XI b) (Simpson, 1949). Results from Grid A show relatively greater diversities of 3.3 and 3.6 for 1977 and 1978 but little diversity of 2.0 for Grid B, 1978. These results show relative degree of dominance of *C. gapperi* in the area rather than overall evenness of the abundance of all species.

(D) Recaptures

C. gapperi, *M. pennsylvanicus*, *P. maniculatus*, and *Z. hudsonius* were not trap shy, and frequently returned to the traps. For example, Figure 11 shows the numbers of recaptures of these hosts on Grid A in 1977 and 1978 and on Grid B in 1978. One vole returned to the traps 13 times between June, 1978 and August, 1978, three times in succession to the same trap, and on the other 10 occasions, to traps in the same vicinity. There was a higher proportion of recaptures on Grid A in 1978 than in 1977. Grid B in 1978 had a higher proportion of recaptures than Grid A in 1977 and 1978.

III. HOST-TICK INTERACTION

(A) Parasite Prevalence, Intensity and Occurrence

On Grid A, 1977, I found 134 mice and voles with 187 larval and 282 nymphal ticks. In 1978 I found 179 mice and voles with 1467 larval and 479 nymphs. Grid B had 40 mice and voles with 20 larvae and 57 nymphs. As numbers were greater on Grid A than on Grid B, and as Grid A was used in 1977 and 1978 my analysis of the tick-host interaction will be based mainly on the data of Grid A, with occasional reference to Grid B.

Tables 4 and 5 show prevalence on Grid A in 1977 and 1978, respectively. Prevalence for all host species infested was 28.6 in 1977 (Table 4) and 37.7 in 1978 (Table 5). Prevalence for each host species for 1977 and 1978, respectively was: *C. gapperi* 31.2 and 41.8, *M. pennsylvanicus* 39.7 and 58.8, *P. maniculatus* 16.7 and 20.7, and *Z. hudsonius* 18.4 and 25.0. These figures show a higher prevalence for each species in 1978 than in 1977. Monthly prevalence for each species in 1977 and 1978 (Tables 4 and 5) show a decreasing percentage of infested hosts, with *C. gapperi* 68.7 in June, 44.0 in July and 5.8 in August, 1977, and 100 in May, 73.7 in June, 60.9 in July and 9.4 in August, 1978. This decrease is related to seasonal pattern of feeding activity as will be shown later.

Table 4. Rodents Trapped From Grid A and Tick Infestation - 1977

Month	Host	Number Trapped	Number Infested	Prevalence %	Number of Larvae and Nymphs	Intensity	Occurrence
June	*C. gapperi*	16	11	68.75	38	3.45	237.19
	M. pennsylvanicus	22	19	86.36	111	5.84	504.34
	P. maniculatus	31	13	41.94	77	5.92	248.28
	Z. hudsonius	7	3	42.86	10	3.33	142.72
July	*C. gapperi*	100	44	44.00	124	2.82	124.08
	M. pennsylvanicus	44	20	45.45	71	3.55	161.35
	P. maniculatus	48	6	12.50	11	1.83	22.88
	Z. hudsonius	14	3	21.43	5	1.67	35.79
August	*C. gapperi*	73	4	5.48	6	1.50	8.22
	M. pennsylvanicus	55	9	16.36	14	1.56	25.52
	P. maniculatus	41	1	2.44	1	1.00	2.44
	Z. hudsonius	17	1	5.88	1	1.00	5.88
Totals	*C. gapperi*	189	59	31.21	168	2.85	88.95
	M. pennsylvanicus	121	48	39.67	196	4.08	161.85
	P. maniculatus	120	20	16.67	89	4.45	74.18
	Z. hudsonius	38	7	18.42	16	2.29	42.18
Total All Species		468	134	28.63	469	3.50	100.21

Table 5. Rodents Trapped From Grid A and Tick Infestation - 1978

Month	Host	Number Trapped	Number Infested	Prevalence %	Number of Larvae and Nymphs	Intensity	Occurrence
May	*C. gapperi*	16	16	100	1018	63.63	6363.0
	M. pennsylvanicus	5	5	100	29	5.80	580.0
	P. maniculatus	4	4	100	72	18.00	1800.0
	Z. hudsonius	18	10	55.56	19	1.90	105.56
June	*C. gapperi*	19	14	73.68	199	14.21	1046.99
	M. pennsylvanicus	22	21	95.45	142	6.76	645.24
	P. maniculatus	12	7	58.33	111	15.86	925.11
	Z. hudsonius	37	10	27.02	13	1.30	35.1
July	*C. gapperi*	64	39	60.94	224	5.74	349.79
	M. pennsylvanicus	34	22	64.71	76	3.45	223.25
	P. maniculatus	26	4	15.38	9	2.85	43.83
	Z. hudsonius	26	7	26.92	8	1.14	30.69
August	*C. gapperi*	85	8	9.41	9	1.13	10.63
	M. pennsylvanicus	36	9	25.0	13	1.44	36.0
	P. maniculatus	40	2	5.0	3	1.50	7.50
	Z. hudsonius	31	1	3.23	1	1.00	3.23
Totals	*C. gapperi*	184	77	41.84	1450	18.83	787.84
	M. pennsylvanicus	97	57	58.76	260	4.56	267.95
	P. maniculatus	82	17	20.73	195	11.47	237.73
	Z. hudsonius	112	28	25.0	41	1.46	36.50
Total All Species		475	179	37.68	1946	10.87	409.58

Intensity for all infested hosts species was 3.5 in 1977 and 10.9 in 1978. Intensity for each host species in 1977 and 1978 was as follows: *C. gapperi* 2.9 and 18.8, *M. pennsylvanicus* 4.08 and 4.56, *P. maniculatus* 4.45 and 11.5, and *Z. hudsonius* 2.3 and 1.5. Intensity data of each host species for each month show decreasing infestation levels in 1977 and 1978. Intensity in *C. gapperi* was 63.6 in May, 14.2 in June, 5.7 in July and 1.1 in August, 1978.

Occurrence on all infested host species in 1977 and 1978 was 100 and 410 respectively and was 89 and 788 for *C. gapperi*, 162 and 268 for *M. pennsylvanicus*, 74.2 and 238 for *P. maniculatus* and 42.2 and 37 for *Z. hudsonius*. Similar to prevalence and intensity, there is a drop in occurrence each month from May to August.

Prevalence, intensity and occurrence data for Grid B appear on Table 6 and all three parameters are low compared to figures from Grid A. Numbers of larvae (Tables 7 and 8) on each host species in 1977 and 1978 were respectively as follows: *C. gapperi* 35 and 1204, *M. pennsylvanicus* 76 and 55, *P. maniculatus* 68 and 189, and *Z. hudsonius* 8 and 27. Number of nymphs for 1977 and 1978 are: *C. gapperi* 133 and 294, *M. pennsylvanicus* 120 and 213, *P. maniculatus* 21 and 15, and *Z. hudsonius* 8 and 14.

In 1977 mean infestations for all species and SE (Tables 7 and 8a) were 156 ± 67.5 and in 1978, 487 ± 236. Mean

Table 6. Rodents Trapped From Grid B and Tick Infestation - 1978

Month	Host	Number Trapped	Number Infested	Prevalence %	Number of Larvae and Nymphs	Intensity	Occurrence
June	*C. gapperi*	71	6	8.45	12	2.0	16.90
	M. pennsylvanicus	4	0	0	0	0	0
	P. maniculatus	30	3	10	8	2.67	26.7
	Z. hudsonius	0	0	0	0	0	0
July	*C. gapperi*	146	25	17.12	47	1.88	32.19
	M. pennsylvanicus	9	4	44.44	8	2.0	88.88
	P. maniculatus	58	1	1.72	1	1.0	1.72
	Z. hudsonius	2	0	0	0	0	0
August	*C. gapperi*	125	1	0.80	1	1.0	0.8
	M. pennsylvanicus	0	0	0	0	0	0
	P. maniculatus	105	0	0	0	0	0
	Z. hudsonius	1	0	0	0	0	0
Totals	*C. gapperi*	342	32	9.37	60	1.88	17.61
	M. pennsylvanicus	13	4	30.77	8	2.0	61.54
	P. maniculatus	193	4	2.07	9	2.95	4.66
	Z. hudsonius	3	0	0	0	0	0
Total All Species		551	40	7.36	77	1.93	14.01

Table 7. Number of Ticks Removed From Rodents - Grid A, 1977

Host Species	June L*	June N*	July L	July N	August L	August N	Total L & N	Mean	±	SE
C. gapperi	5	33	29	95	1	5	168	56.0		35.2
M. pennsylvanicus	64	47	11	60	1	13	196	65.3		28.1
P. maniculatus	65	12	3	8	0	1	89	29.6		23.8
Z. hudsonius	6	4	2	3	0	1	16	5.3		2.6
Total	140	96	45	166	2	20	469	156.3		67.5

L* - Larvae

N* - Nymphs

Table 8. Number of Ticks Removed From Rodents: (a) Grid A 1978, (b) Grid B 1978

	May		June		July		August		Total	Mean	±	SE
	L*	N*	L	N	L	N	L	N	L + N			
(a) Grid A												
C. gapperi	1016	2	174	25	11	213	3	6	1450	362.5		223.7
M. pennsylvanicus	17	12	30	112	3	73	5	8	260	65.0		28.9
P. maniculatus	72	-	109	2	-	9	-	3	195	48.8		25.9
Z. hudsonius	17	2	9	4	1	7	-	1	41	10.3		3.8
Total	1122	16	322	143	15	302	8	18	1946	486.5		235.5
(b) Grid B												
C. gapperi	-	-	12	-	-	47	-	1	60	15		11.0
M. pennsylvanicus	-	-	-	-	-	8	-	-	8	2		2.0
P. maniculatus	-	-	8	-	-	1	-	-	9	2.3		1.9
Z. hudsonius	-	-	-	-	-	-	-	-	-	-		-
Total	-	-	20	-	-	56	-	1	77	19.3		13.1

L* - Larvae

N* - Nymphs

infestation and SE of each host species in 1977 and 1978 respectively were: C. gapperi 56.0 ± 35.2 and 363 ± 223.7, M. pennsylvanicus 65.3 ± 28.1 and 65.0 ± 28.9, P. maniculatus 29.6 ± 23.8 and 48.8 ± 25.9 and Z. hudsonius 5.3 ± 2.6 and 10.3 ± 3.8. Grid B results appear in Table 8(b).

Adult ticks infested larger mammals (Table 2). Of the 75 squirrels examined for the presence of ticks (Table 1) prevalence was 32.5% and intensity 1.64, with an occurrence of 53.3. Infested S. franklinii on Grid A were 3 in 1977 and 18 in 1978. One M. mephitis in 1977 had 25 engorging adult ticks, and another in 1978 had over 38. Seventeen engorging adult ticks were removed from one P. lotor in 1978. M. erminea and M. frenata had low levels of infestation as with the ground squirrels.

No larvae or nymphs were found on larger mammals. Neither immature nor adult ticks were found on S. cinereus. This could be the result of 100% mortality of S. cinereus in traps during the night. Ticks could have crawled out of the traps.

(B) Host Recaptures and Reinfestations

Many mice and voles were captured more than once during the study. In 1977 one C. gapperi was captured 11 times.

On the first occasion it carried nine larvae and six nymphs. These were removed before the vole was released. Fifteen days later the same vole was recaptured and found to be carrying 12 larvae which were removed. Three days later the vole was again recaptured and one larva and 31 nymphs removed. On two other occasions it was recaptured and four and five nymphs respectively were removed.

Some of the recaptures were not reinfested. Seasonal infestation frequency distributions (Fig. 12 to 19) show the rate of infestation levels in the recaptured hosts. The fluctuations in these results resemble infestations of first catches. The level of reinfestation was low in 1977. C. gapperi (Fig. 12), the only rodent hosts to show higher level of reinfested recaptured hosts than other mice and voles, had two voles with 10 larvae and nymphs on July 19th and two voles with seven larvae and nymphs on July 21st. Reinfestation declined but recaptured host numbers rose until August 3rd when they started to decrease. M. pennsylvanicus (Fig. 13) was next with two hosts carrying four ticks on July 19th. Recaptured host numbers increased but ticks declined. Reinfestation on P. maniculatus (Fig. 14) and Z. hudsonius (Fig. 15) was negligible. Recaptured mice and voles in Figures 12, 13, 14 and 15 show normal distribution.

In 1978, reinfestation of recaptures was highest in C. gapperi (Fig. 16). One vole first caught on May 17th

Figure 12. Seasonal infestation levels of *D. variabilis* larvae and nymphs on *C. gapperi*, Grid A, 1977.

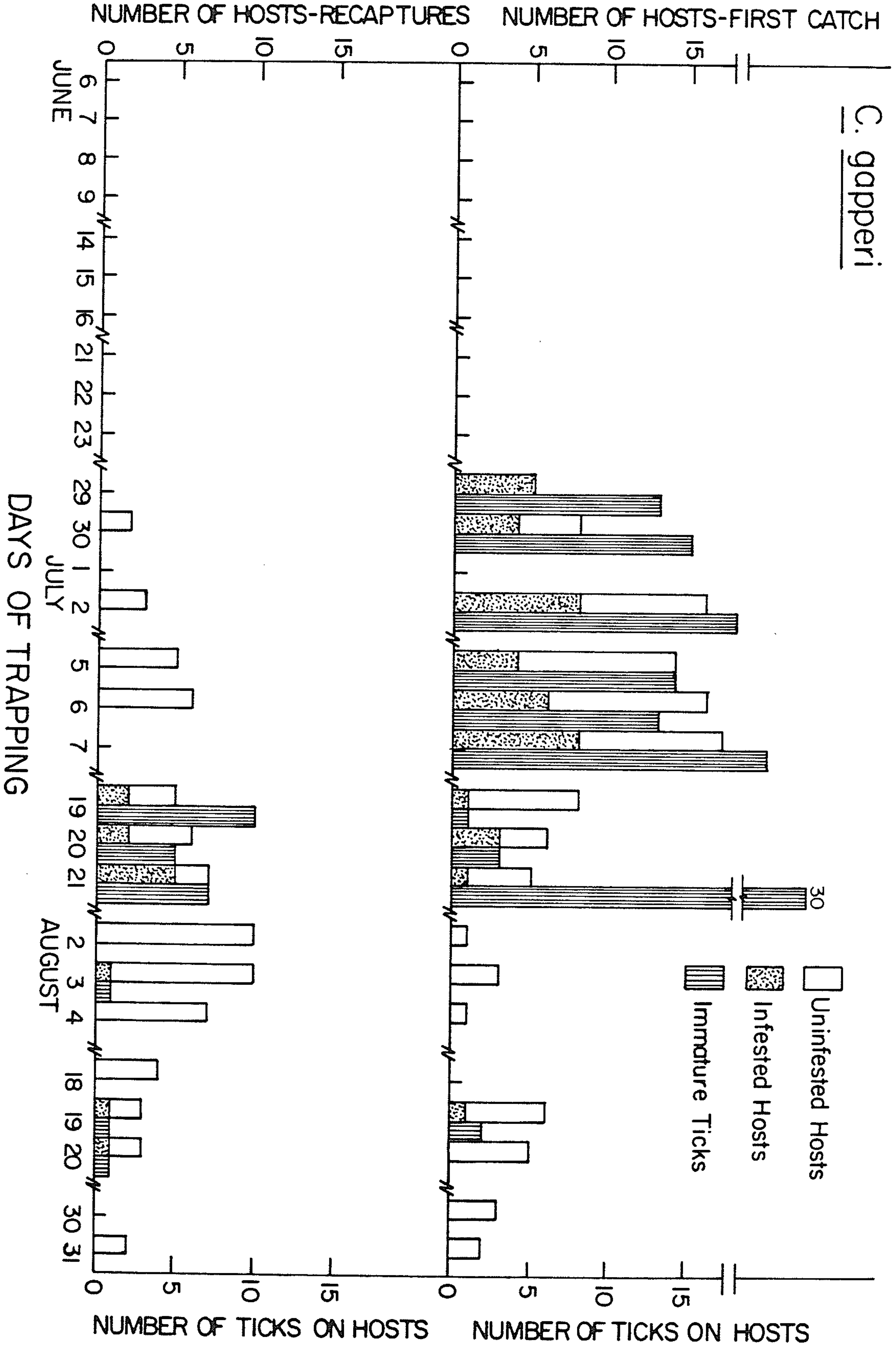

C. gapperi
Uninfested Hosts
Infested Hosts
Immature Ticks
NUMBER OF HOSTS-FIRST CATCH
NUMBER OF HOSTS-RECAPTURES
NUMBER OF TICKS ON HOSTS
NUMBER OF TICKS ON HOSTS
0
5
10
15
30
DAYS OF TRAPPING
JUNE
6 7 8 9 14 15 16 21 22 23 29 30
JULY
1 2 5 6 7 19 20 21
AUGUST
2 3 4 18 19 20 30 31

Figure 13. Seasonal infestation levels of *D. variabilis* larvae and nymphs on *M. pennsylvanicus*, Grid A, 1977.

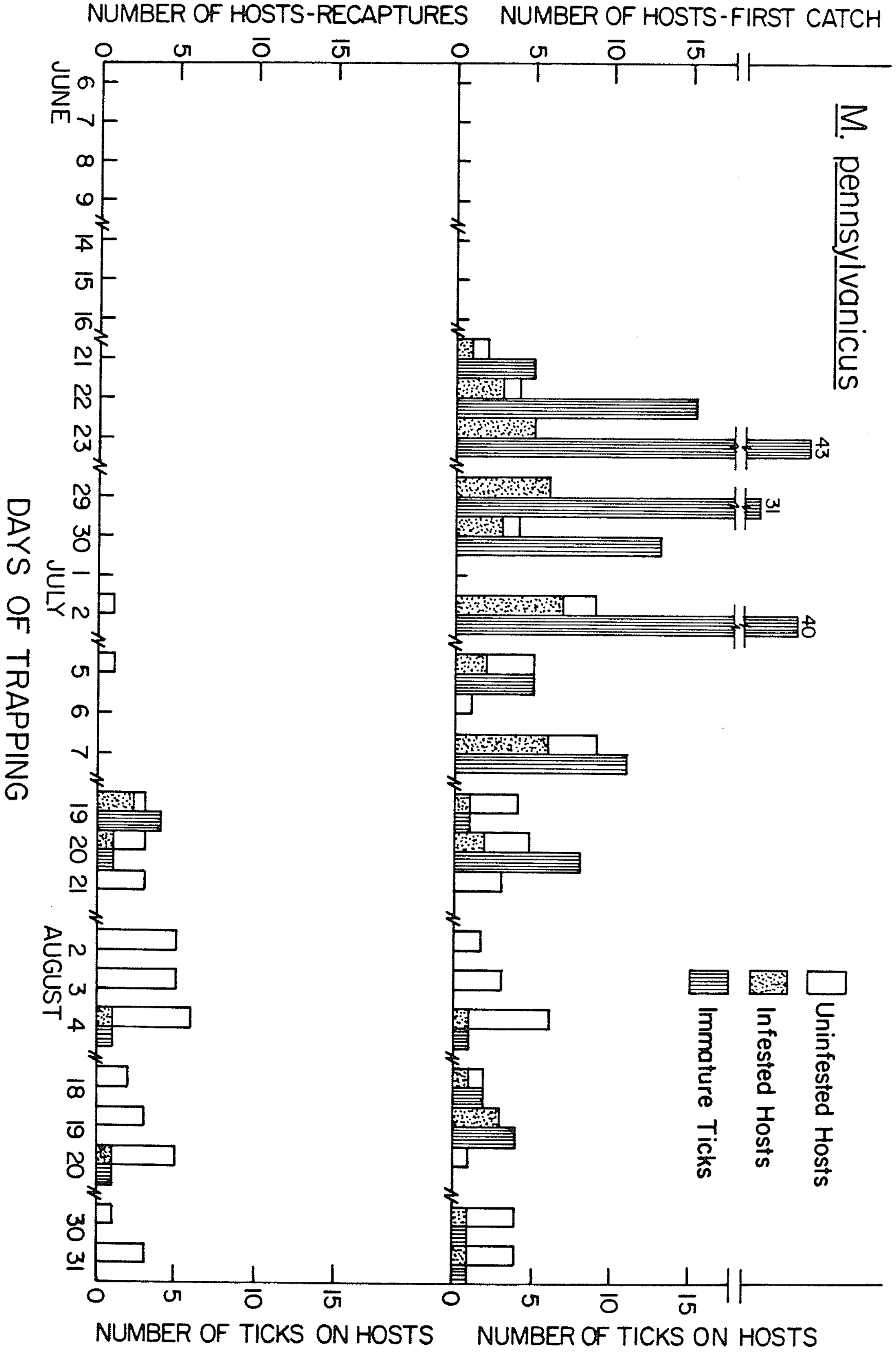

M. pennsylvanicus
Uninfested Hosts
Infested Hosts
Immature Ticks
NUMBER OF HOSTS-FIRST CATCH
NUMBER OF HOSTS-RECAPTURES
NUMBER OF TICKS ON HOSTS
NUMBER OF TICKS ON HOSTS
0
5
10
15
43
31
40
JUNE
6 7 8 9 14 15 16 21 22 23 29 30
JULY
1 2 5 6 7 19 20 21
AUGUST
2 3 4 18 19 20 30 31
DAYS OF TRAPPING

Figure 14. Seasonal infestation levels of *D. variabilis* larvae and nymphs on *P. maniculatus*, Grid A, 1977.

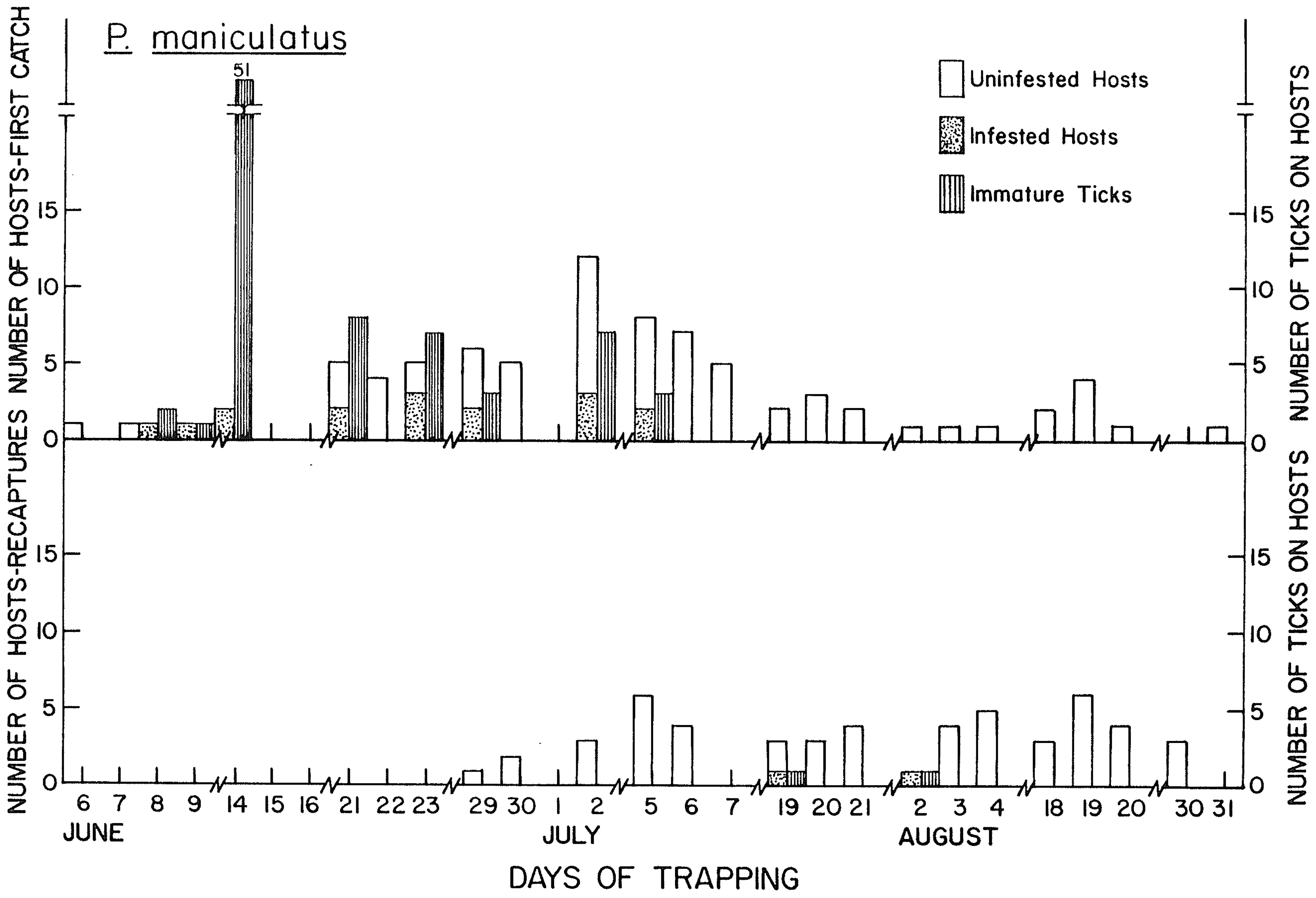

P. maniculatus
Uninfested Hosts
Infested Hosts
Immature Ticks
51
NUMBER OF HOSTS-RECAPTURES NUMBER OF HOSTS-FIRST CATCH
NUMBER OF TICKS ON HOSTS
NUMBER OF TICKS ON HOSTS
0
5
10
15
6 7 8 9 14 15 16 21 22 23 29 30 1 2 5 6 7 19 20 21 2 3 4 18 19 20 30 31
JUNE
JULY
AUGUST
DAYS OF TRAPPING

Figure 15. Seasonal infestation levels of _D_. _variabilis_ larvae and nymphs on Z. _hudsonius_, Grid A, 1977.

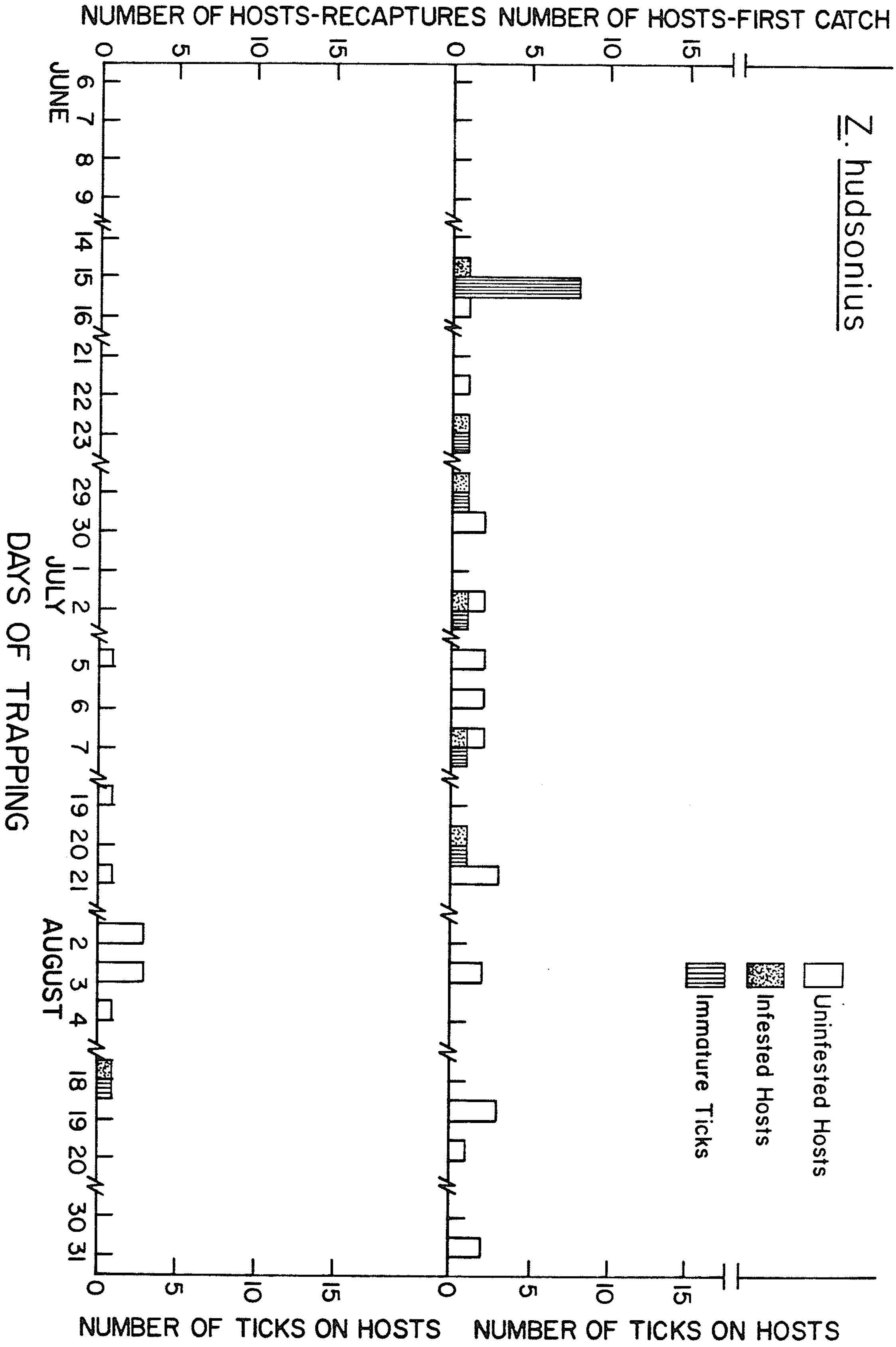

Z. hudsonius
NUMBER OF HOSTS-RECAPTURES
NUMBER OF HOSTS-FIRST CATCH
NUMBER OF TICKS ON HOSTS
NUMBER OF TICKS ON HOSTS
0
5
10
15
JUNE
6 7 8 9 14 15 16 21 22 23 29 30
JULY
1 2 5 6 7 19 20 21
AUGUST
2 3 4 18 19 20 30 31
DAYS OF TRAPPING
Uninfested Hosts
Infested Hosts
Immature Ticks

Figure 16. Seasonal infestation levels of *D. variabilis* larvae and numphs on *C. gapperi*, Grid A, 1978.

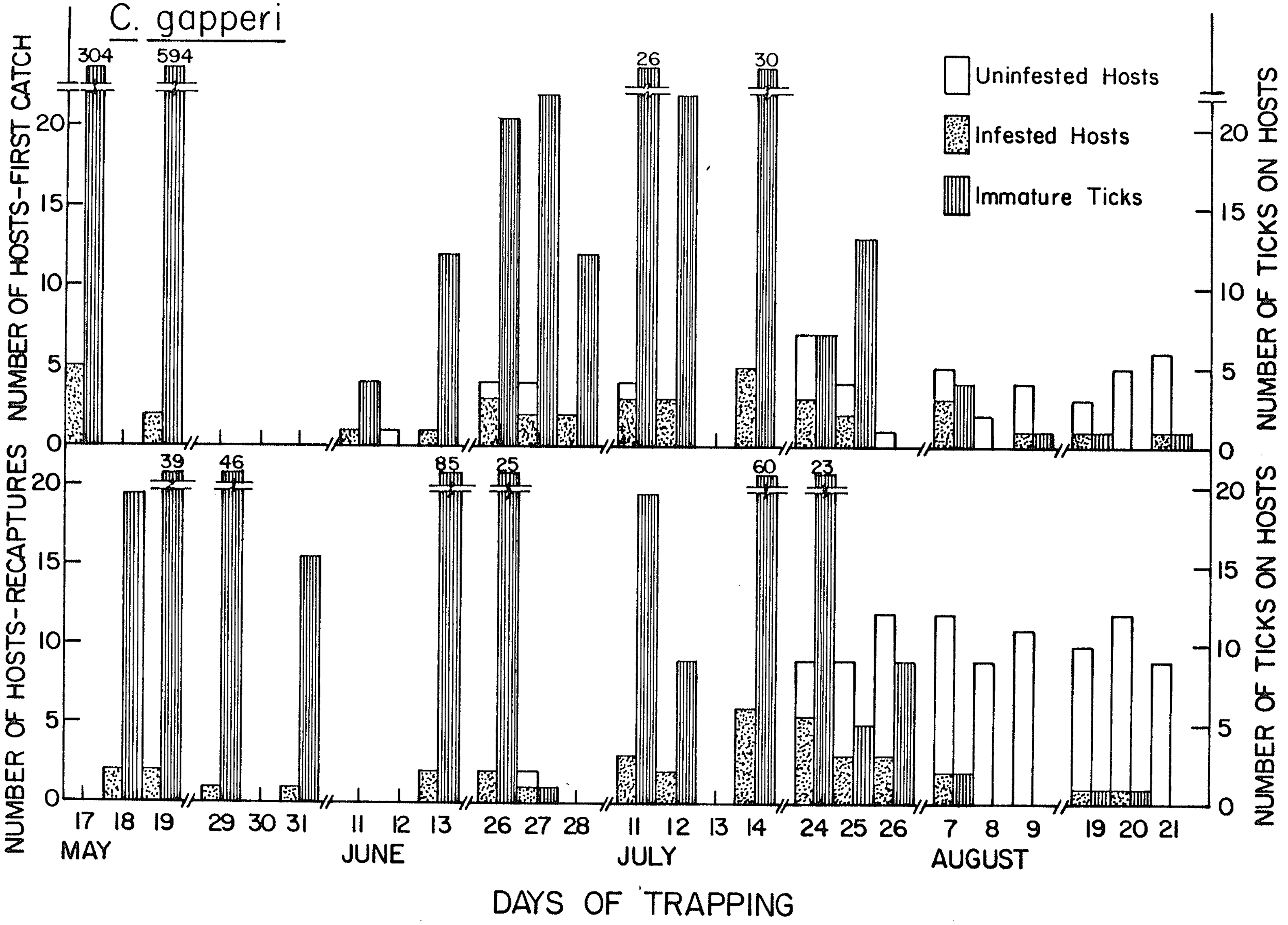

C. gapperi
Uninfested Hosts
Infested Hosts
Immature Ticks
NUMBER OF HOSTS-FIRST CATCH
NUMBER OF HOSTS-RECAPTURES
NUMBER OF TICKS ON HOSTS
NUMBER OF TICKS ON HOSTS
0
5
10
15
20
304
594
26
30
39
46
85
25
60
23
17
18
19
29
30
31
11
12
13
26
27
28
11
12
13
14
24
25
26
7
8
9
19
20
21
MAY
JUNE
JULY
AUGUST
DAYS OF TRAPPING

Figure 17. Seasonal infestation levels of *D. variabilis* larvae and nymphs on *M. pennsylvanicus*, Grid A, 1978.

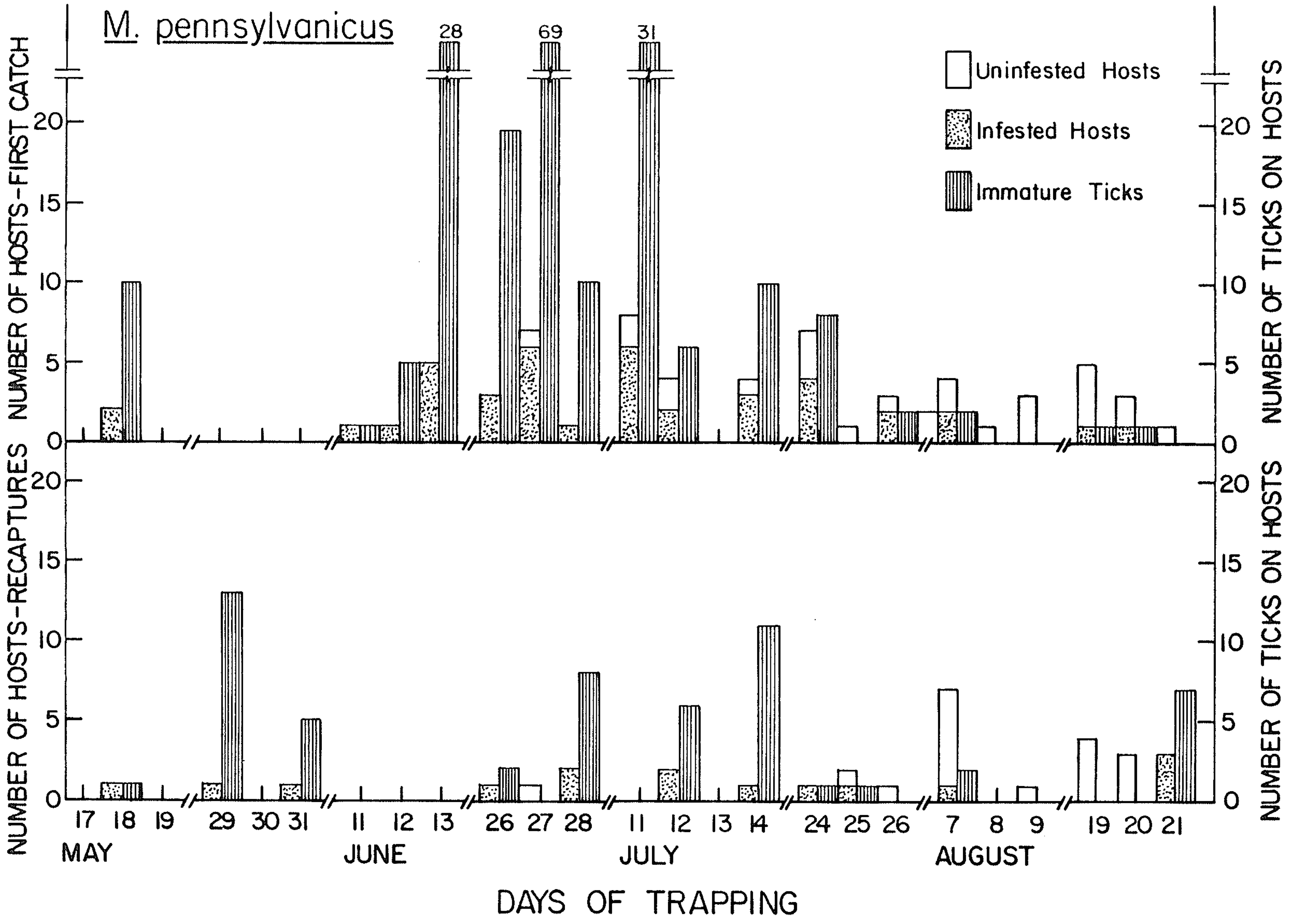

M. pennsylvanicus
Uninfested Hosts
Infested Hosts
Immature Ticks
NUMBER OF HOSTS-FIRST CATCH
NUMBER OF HOSTS-RECAPTURES
NUMBER OF TICKS ON HOSTS
NUMBER OF TICKS ON HOSTS
0
5
10
15
20
28
69
31
17
18
19
29
30
31
11
12
13
26
27
28
11
12
13
14
24
25
26
7
8
9
19
20
21
MAY
JUNE
JULY
AUGUST
DAYS OF TRAPPING

Figure 18. Seasonal infestation levels of *D. variabilis* larvae and nymphs on *P. maniculatus*, Grid A, 1978.

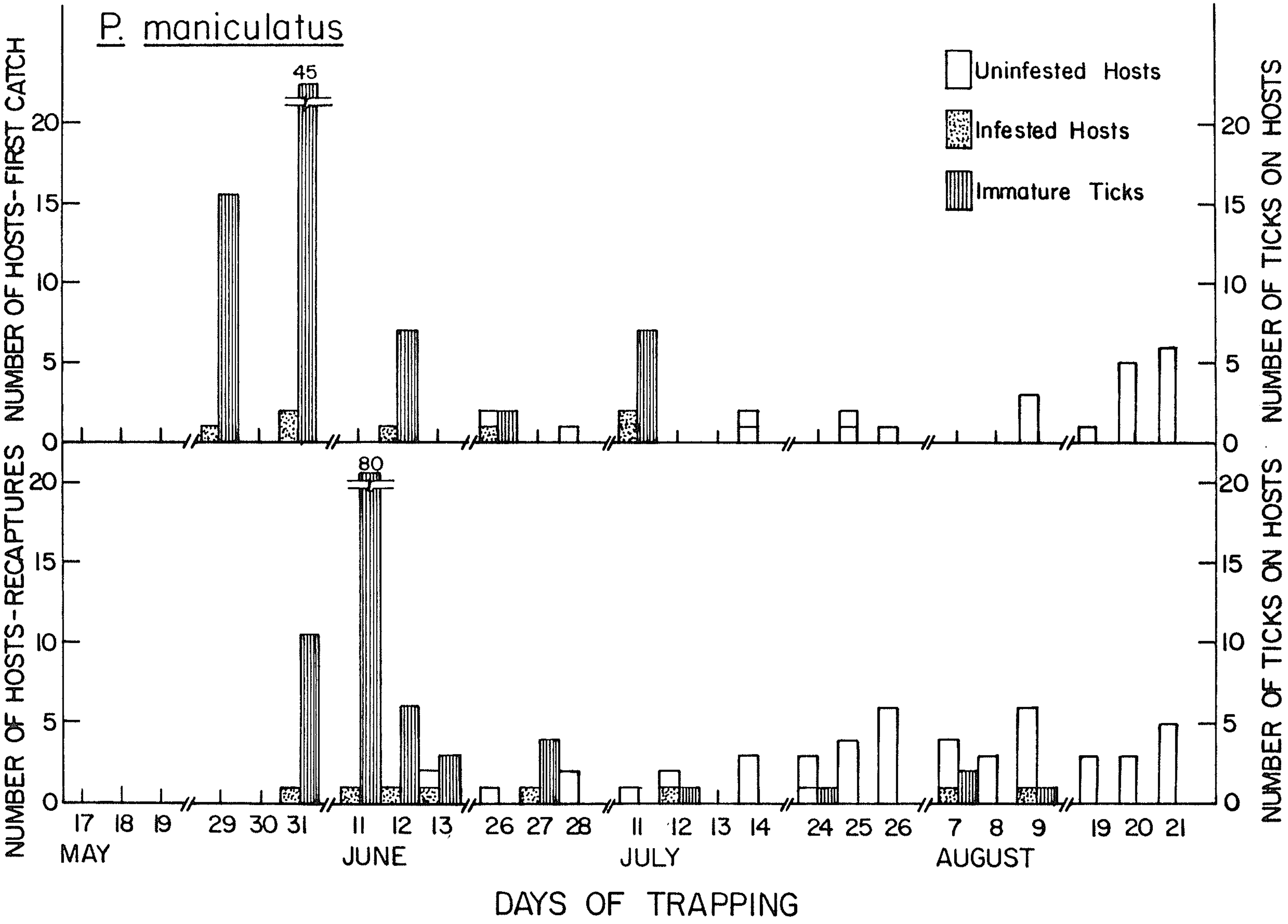
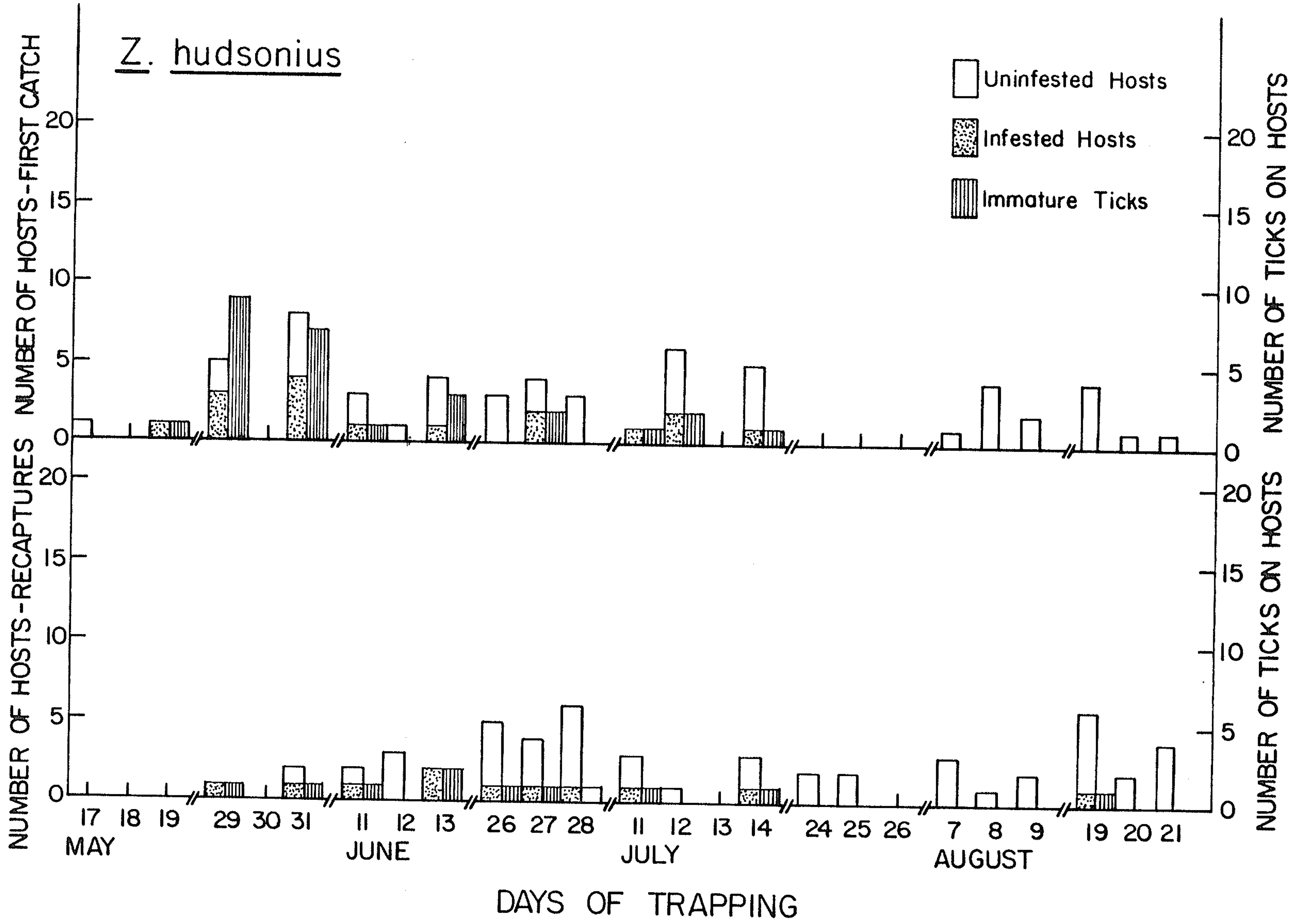

P. maniculatus
Uninfested Hosts
Infested Hosts
Immature Ticks
45
80
NUMBER OF HOSTS-FIRST CATCH
NUMBER OF HOSTS-RECAPTURES
NUMBER OF TICKS ON HOSTS
NUMBER OF TICKS ON HOSTS
0
5
10
15
20
17 18 19 29 30 31
MAY
11 12 13 26 27 28
JUNE
11 12 13 14 24 25 26
JULY
7 8 9 19 20 21
AUGUST
DAYS OF TRAPPING

Figure 19. Seasonal infestation levels of *D. variabilis* larvae and nymphs on *Z. hudsonius*, Grid A, 1978.



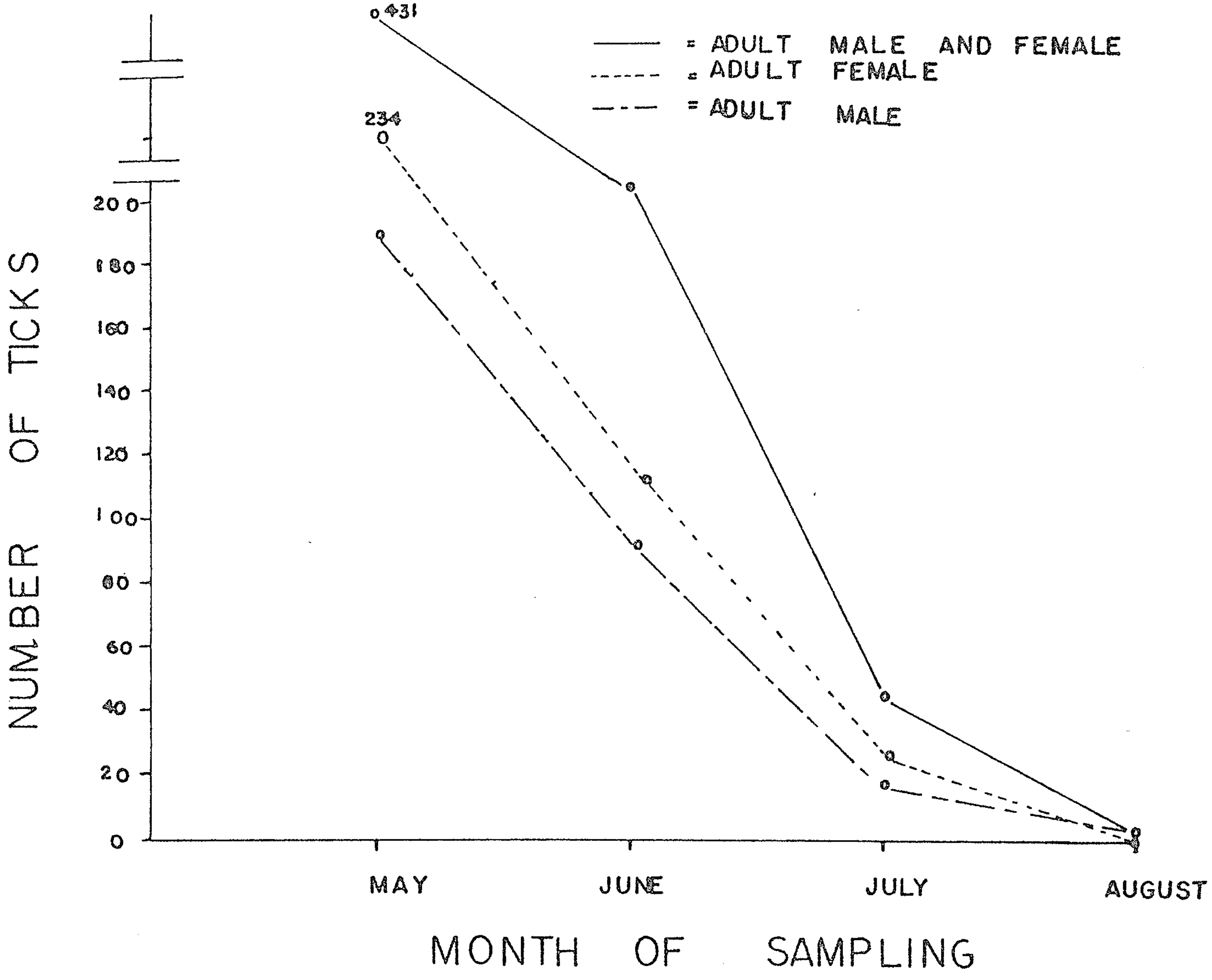
Z. hudsonius
Uninfested Hosts
Infested Hosts
Immature Ticks
NUMBER OF HOSTS-FIRST CATCH
NUMBER OF HOSTS-RECAPTURES
NUMBER OF TICKS ON HOSTS
NUMBER OF TICKS ON HOSTS
0
5
10
15
20
17
18
19
29
30
31
MAY
11
12
13
26
27
28
JUNE
11
12
13
14
24
25
26
JULY
7
8
9
19
20
21
AUGUST
DAYS OF TRAPPING

was recaptured on May 18th and carried 19 larvae and nymphs. On June 13th, two recaptured voles were infested with 85 larvae and nymphs. Reinfestation remained high until July 24th, when the level declined. *M. pennsylvanicus* (Fig. 17) and *P. maniculatus* (Fig. 18) were next with fairly moderate levels of infestation. Infestation level was maintained until August in *M. pennsylvanicus* but in *P. maniculatus*, there was a sharp drop from June 11th. Recaptured host numbers were low in *M. pennsylvanicus* and *P. maniculatus*. *Z. hudsonius* (Fig. 19) had the lowest infestation level of all mice and voles.

(C) Frequency Distribution of Immature Ticks

Tables 7 and 8 show observed distribution numbers of larvae and nymphs on hosts on Grid A in 1977 and 1978. *M. pennsylvanicus* was the most heavily infested of all rodent hosts in 1977 with mean number 65.3 ± 28.1 SE for larvae and nymphs. Second was *C. gapperi* with $\bar{x}$: SE 56.0 ± 35.2, followed by *P. maniculatus* with $\bar{x}$: SE 29.6 ± 23.8 and *Z. hudsonius* $\bar{x}$: SE 5.3 ± 2.6. In 1978, Grid A, *C. gapperi* was highest with $\bar{x}$: SE 362.5 ± 223.7, followed by *M. pennsylvanicus* $\bar{x}$: SE 65 ± 28.9, *P. maniculatus* $\bar{x}$: SE 48.8 ± 25.9 and finally *Z. hudsonius* $\bar{x}$: SE 10.3 ± 3.8.

Figure 20. Seasonal variation of adult *D*. *variabilis* ticks on vegetation, 1978.


431
234
— = ADULT MALE AND FEMALE
- - - = ADULT FEMALE
— · — = ADULT MALE
NUMBER OF TICKS
200
180
160
140
120
100
80
60
40
20
0
MAY
JUNE
JULY
AUGUST
MONTH OF SAMPLING

In each distribution, variances were greater than the means. I conclude that the distribution of ticks on hosts was not random. The significance of the difference of the observed variance : mean ratios were tested with a t-test. With one degree of freedom results gave a $t > 10.6$ and $P < 0.005$. Results show that observed frequency distributions are significantly different from random distributions. Crofton (1971a) suggested that the frequently observed clumped distributions can be described by a negative binomial distribution which is defined by the arithmetic mean and the exponent K. Expected distribution was calculated and the X^2 test for goodness of fit applied. Results show no significant difference between observed and expected distributions. These results confirm that ticks are non-randomly distributed throughout the sampled population.

(D) Seasonal Pattern of Feeding Activity in *D. variabilis*

In 1977, field observations started on June 6th and continued until August 31st. Feeding of larvae, nymphs and adult ticks occurred throughout this period. In 1978 field observations started on May 17th and continued until August 21st. Feeding occurred throughout this period and as in 1977, evidence of feeding depended on the capture of rodents which varied with each species of host. Adult *D. variabilis* seasonal pattern of activity (Fig. 20) was observed through vegetation flagging data.

Numbers of hosts captured, and the number infested plus the mean number of immature ticks per host for the four major hosts captured on Grid A in 1977 and 1978 appear in Table 4 and Table 7, respectively and similar results for Grid B, 1978, are in Tables 5 and 8. Figure 12 to Figure 19 show tick infestation levels of individual host species captured for the first time, and for the recaptured hosts on Grid A in 1977 and 1978. Both years of sampling showed the same seasonal patterns for each host, though the level of infestation differed with each species.

1. Larvae

The first larvae were found on *P. maniculatus* on June 8th and on all other kinds of hosts by June 27th, 1977. In 1978 *C. gapperi*, *M. pennsylvanicus* and *Z. hudsonius* were infested on May 17th, but it was 12 days later before the first *P. maniculatus* were found infested on May 29th.

The feeding of larval ticks of all four rodent species was unimodal in 1977. Peak feeding in *C. gapperi* and *M. pennsylvanicus* occurred in late June and the first half of July whereas the peak fell in early June for *P. maniculatus* and late May in *Z. hudsonius*. The peaks for all four rodents occurred at almost identical times in 1978 as in 1977. In 1978 *C. gapperi* may have had two peaks, the one discussed above and one in mid-May but unfortunately no *C. gapperi* were captured in late May. Data from the recaptures show a high incidence of feeding at this time.

The magnitude of the peak was greatest in C. gapperi followed by M. pennsylvanicus, P. maniculatus and Z. hudsonius in decreasing order in 1977. The four species were in the same order of decreasing magnitude in 1978. It is also apparent that the peaks were more concentrated in 1977 than in 1978.

There were 12 larvae in June on C. gapperi on Grid B, 1978 and eight on P. maniculatus (Table 8b). Z. hudsonius and M. pennsylvanicus were not infested. There were no larvae on this grid in July and August.

2. Nymphs

The first feeding nymphs were recorded on Z. hudsonius on June 15th and on the other major hosts by June 23rd, 1977. In 1978, C. gapperi and M. pennsylvanicus were infested on May 17th and Z. hudsonius by 31st May, but P. maniculatus was found infested on June 26th. The magnitude of the nymphal peaks was much less than those of the larvae. Lesser number of nymphs reflects the mortality to which the larvae are exposed. The last feeding nymphs were in mid-August on C. gapperi and M. pennsylvanicus. Feeding nymphs were not found on P. maniculatus after July 5th and on Z. hudsonius after July 20th in 1977. The pattern was almost identical in 1978 with last feeding activity in a *Z. hudsonius* recapture on 18th August in 1978 and and 19th August, in 1978. It is interesting to note that the time of the last feeding activity occurred later in *C. gapperi* and *M. pennsylvanicus* in 1977 and 1978.

C. gapperi had 47 nymphs in July, *M. pennsylvanicus* eight, *P. maniculatus* one and *Z. hudsonius* was not infested.

Seasonal feeding patterns (Fig. 21 and 22) show peak periods of feeding. In 1977 larvae were abundant in June and declined in numbers thereafter. Nymphs increased from June and reached a peak in July, then started to decline and had almost disappeared by August. In 1978 the pattern was the same but peaks for larvae were in May and June. The position of the nymphs was the same as the previous year.

3. Adults

The first feeding adult was found on a *S. franklinii* on June 21st, 1977 and the last on *M. erminea* on August 19th, 1977. Adult tick feeding occurred throughout this period. In 1978 the first feeding adult was found on *S. franklinii* on May 11th and the last on *P. lotor* on 22nd August. First evidence of tick activity was observed on humans in

Figure 21. Seasonal feeding pattern of *D. variabilis* larvae and nymphs on Grid A in 1977.

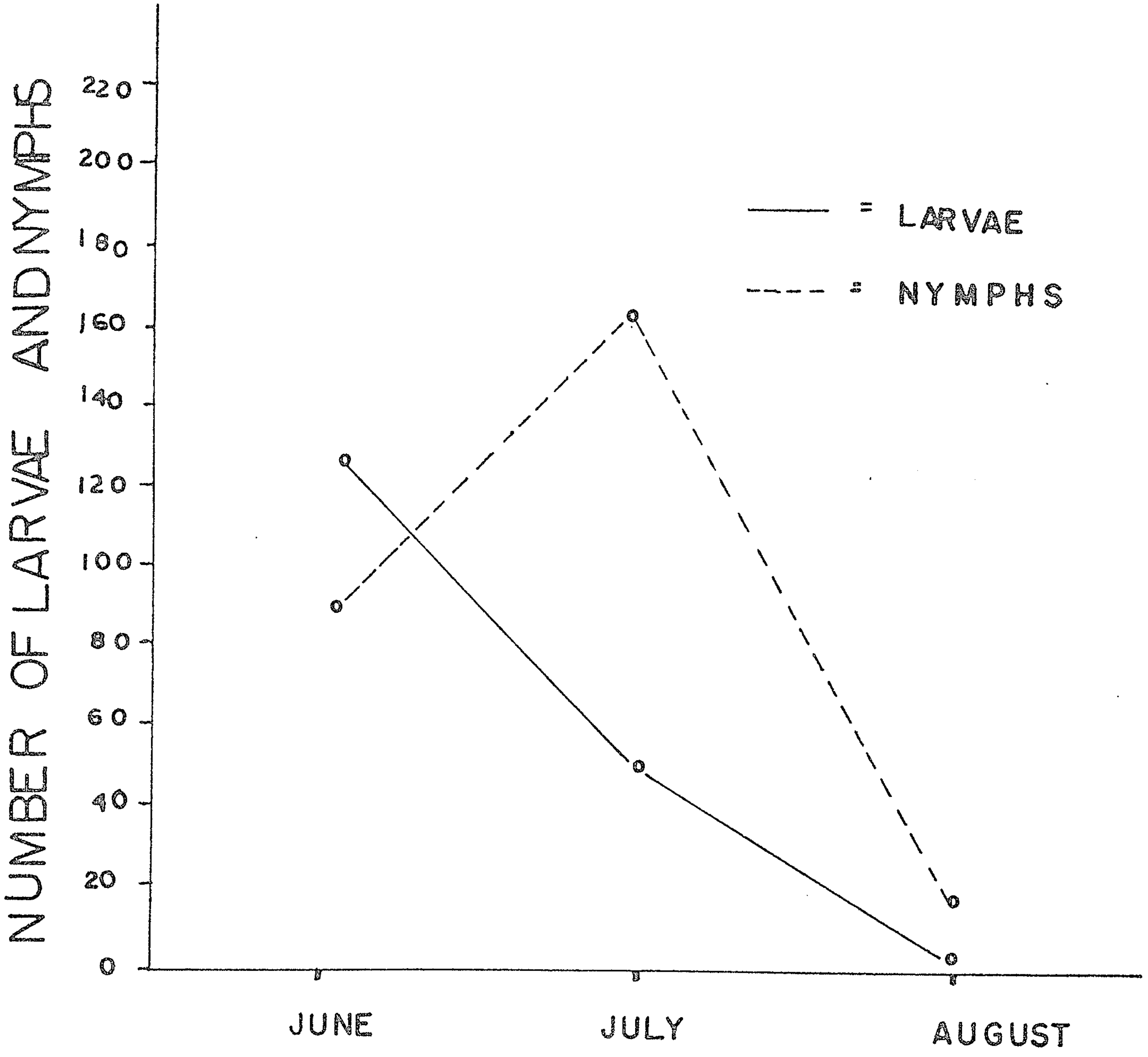
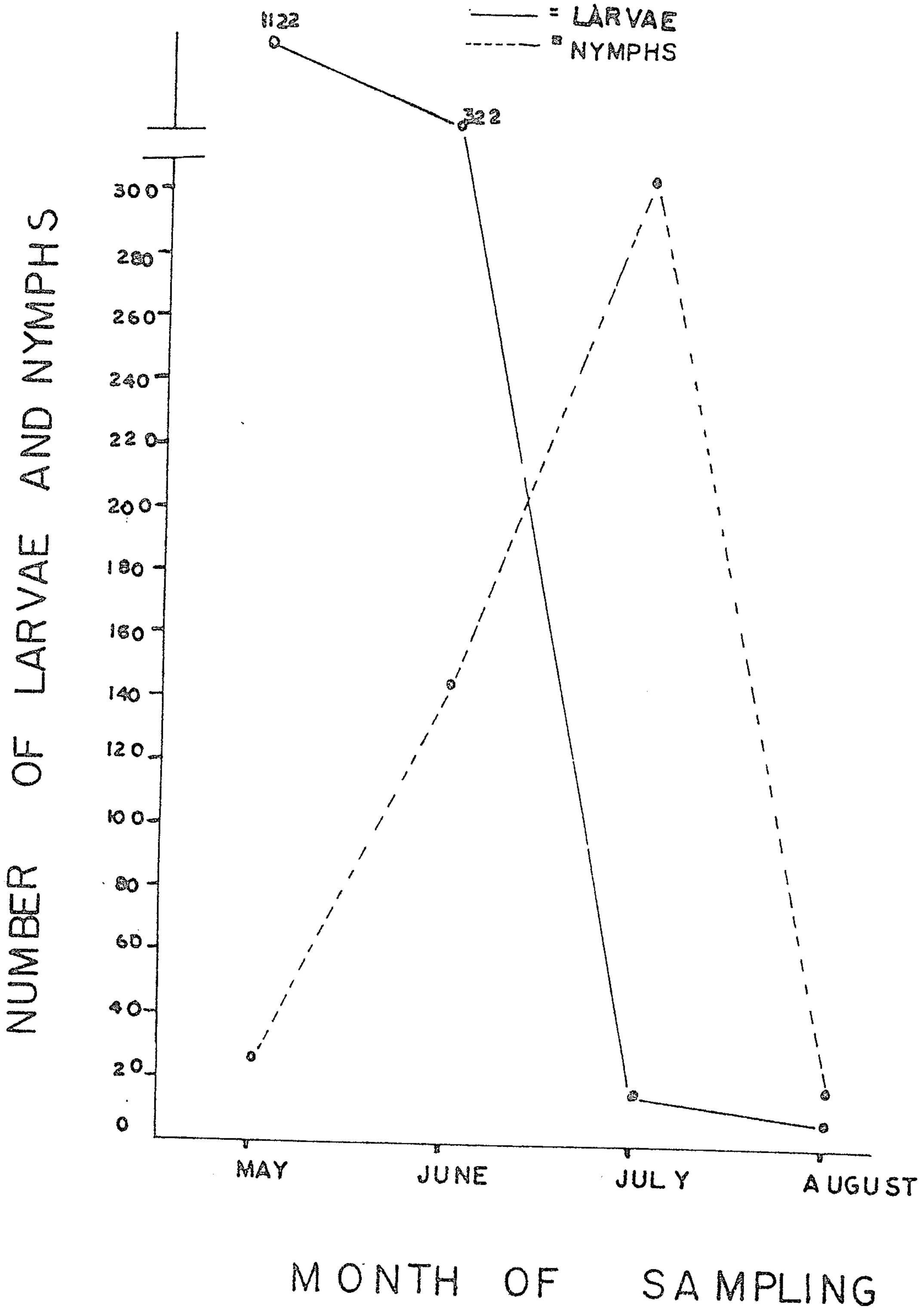

NUMBER OF LARVAE AND NYMPHS
220
200
180
160
140
120
100
80
60
40
20
0
JUNE
JULY
AUGUST
—— = LARVAE
- - - - = NYMPHS

Figure 22. Seasonal feeding pattern of *D. variabilis* larvae and nymphs on Grid A in 1978.



1122
322
= LARVAE
= NYMPHS
300
280
260
240
220
200
180
160
140
120
100
80
60
40
20
0
NUMBER OF LARVAE AND NYMPHS
MAY
JUNE
JULY
AUGUST
MONTH OF SAMPLING

1977 and 1978. Unfortunately, dates were not recorded. Figure 20 indicates that the highest number of questing adults in 1978 occurred in the second fortnight of May. The much lower incidence of adults compared to larvae is noteworthy. The difference between feeding nymphs and adults is not as great as that between larvae and nymphs.

IV. LIFE CYCLE STUDIES IN THE LABORATORY ON *D. variabilis*

Fresh ticks were collected from the field, taken to the laboratory and placed on rats or rabbits to engorge. Weight of engorged females averaged 0.625 ± 0.001 gm. Mean number of eggs laid was 6500 ± 150, range 4,000 to 7,900. Preoviposition period was 5 days and the period of oviposition was 27 days. Period before hatching was 28 days (Table 9).

Ticks collected in the field at the peak of questing in 1977 and held in the refrigerator for two months at 40°C took several days to attach but after 14 days were only partially engorged. In feeding experiments in 1978 all of the ticks attached on hosts within 12 hours and were fully engorged in 4-7 days. Percentage hatch in all egg clutches was >95%. A high level of larval mortality was experienced by Randolph (1975b). I found mortality of approximately 30% in the first 18 days, but survival rate increased.

Table 9 . *D. variabilis* development: oviposition.

Factor (n = 48)	Mean ± SE	Range
Period of engorging in days	5	4 - 7
Weight of engorged female	0.625 ± 0.001 gm	0.09 - 0.9 gm
Eggs laid (range)*	6,500 ± 149.5	4,000 - 7,900
Preoviposition period in days	5	3 - 12
Period of oviposition in days	27	24 - 33
Period before hatching in days	28	26 - 31

Percentage hatch in all egg masses was greater than 95%.

* n = 24.

In this study an average period of two months 16 days was required from the beginning of engorgement to the end of hatching. Life cycle studies were not carried beyond the larval stage. Engorged nymphs from field mice, removed and kept under laboratory conditions, moulted within an average period of 36 days.

A. Parthenogenesis

Ten female ticks collected from grass blades in the field were placed on hosts. No male ticks were included. Ticks attached and engorged but the rate of feeding was slow. Ticks took an average of 8 days to feed but weighed much less than females with males on the same host. Oviposition took place but total egg clutches were about 25% of the normal. Eggs left in the environmental chamber for two months, but none hatched.

V. WINTER INVERTEBRATE TRAPPING

Invertebrates caught in the winter traps were examined to find if any ticks were present. No ticks were found in all samples from trap sites in different vegetation habitats of Low Grass, Tall Grass, Edge of Woods, Woods and Mixed herbs and shrubs. There were high densities of other invertebrates which were only identified to Order. The following Orders were present: Acarina, Araneae, Colembola, Coleoptera, Diptera, Hymenoptera, Orthoptera, Lepidoptera, Neuroptera and Thysanoptera. Mites, spiders and beetles composed more than 50% of the species present. Three *Sorex cinereus* were also collected.

Heavy snow fell two days after the traps were set in the field. From the high numbers of invertebrates collected in the traps, it was evident that much activity occurs under the snow. Ticks were apparently not part of this activity. Samples of litter collected around the traps also revealed high numbers of mites.

VI. VEGETATION STUDIES

Twenty-four species of plants were recorded in the random quadrats sampled in Grid A, 11 species in the short grass, 15 in the tall grass, and 17 at the edge of wood. Six species were found in all three habitats (Table 10). Density, frequency and cover was recorded for each species (Table 10).

Table 10 . Plant species in study area showing Mean Density, Frequency and Dominance Analyses. (n = 20)

Species	Low Grass Density	Low Grass Frequency %	Low Grass Dominance %	Tall Grass Density	Tall Grass Frequency %	Tall Grass Dominance %	Edge of Woods Density	Edge of Woods Frequency %	Edge of Woods Dominance %
B. inermis	20.9	80	24.1	80.7	100	70.9	109	65	47.1
C. canadensis	61.2	90	32.4	20.1	50	12.3	77.1	80	32.5
S. asper	1.6	55	9.5	1.3	50	4.8	0.9	65	4.2
A. brachyactis	2.6	70	6.8	1.0	20	1.1	0.05	5	1.3
R. maritimus var fueginus				0.4	5	1.0			
P. anserina				1.3	5	1.0	0.2	5	0.3
P. coccineum				0.1	10	0.3			
S. occidentalis	1.5	35	5.2	0.1	5	0.1	0.4	10	4.5
R. laciniata				0.05	5	0.3	0.05	5	0.5
M. arvensis				0.05	5	0.1			
A. negundo				0.2	5	0.3	0.05	5	1.3
R. oxycanthoides				0.1	10	0.3			
R. blanda				0.05	5	0.1			
A. absinthium	0.6	10	0.3	0.1	5	3.8			
C. arvense	1.8	85	13.7	1.0	40	3.7	1.2	55	2.2
P. quinquefolia	0.1	10	0.1						
R. idaeus	0.5	15	3.0				0.2	15	2.3
M. alba	0.4	10	0.9				0.4	10	0.6
A. pansus	0.7	5	1.5				0.8	15	0.7
Chenopodium spp.							0.7	30	0.9
A. repens							0.3	5	0.1
H. annuus							0.8	35	4.4
F. pennsylvanica							0.2	10	1.5
S. canadensis									

Density and cover (dominance) of B. inermis and C. canadensis was significantly higher than that for any other species. B. inermis had the highest density (109 plants/m^2) at the edge of the woods and <80 plants/m^2 in the tall grass. It also had the highest cover value (70.9%) in the tall grass. C. canadensis had a density of 77 plants/m^2 in the edge of woods and 61.2 plants/m^2 in the short grass, with cover values of 32.5% and 32.4% at the edge of woods and short grass respectively. The rest of the species had densities ranging from 0.1 to 2.6 plants/m^2 and cover values, range 0.1 - 13.7%.

B. inermis had the highest frequency value (100%) in the tall grass, 80% in the short grass, and 65% in the edge of woods. C. canadensis was second highest with 90% in the short grass, 80% in the edge of woods, and 50% in the tall grass. Other species had frequency values ranging from 5% to 70%.

Importance values (IV's) were calculated for each species in the quadrats in order to describe the three habitats (Table 11). The Importance Value being the sum of the relative density, relative frequency and relative dominance, has a maximum value of 300. B. inermis had the highest IV of any species in the tall grass (IV = 178.1) and wood margin (IV = 114.8) with C. canadensis next in importance with IV's of 119.6 in the short grass, 89.7 in the edge of woods. S. asper and C. arvense had IV's greater than 10 in all

Table 11. Importance Values (IV) of plant species from Low grass, Tall grass and Edge of Woods.

Plant Species	Low Grass	Tall Grass	Edge of Woods
Bromus inermis	64.7	178.1	114.8
Calamagrostis canadensis	119.6	46.8	89.7
Sonchus asper	23.2	21.6	19.7
Potentilla anserina		3.8	1.6
Aster brachyactis	24.9	8.3	2.4
Cirsium arvense	34.3	17.1	15.6
Rumex maritimus		3.0	
Acer negundo		2.0	2.4
Polygonum coccineum		3.5	
Symphoricarpos occidentalis	14.4	1.8	6.8
Ribes oxycanthoides		3.5	
Artemisia absinthium	3.1	5.5	
Rudbeckia laciniata		2.0	1.3
Mentha arvensis		1.8	
Rosa blanda		1.8	
Parthenocissus quinquefolia	2.4		
Rubus idaeus	6.8		5.7
Melilotus alba	3.5		3.2
Aster pansus	3.4		4.5
Chenopodium spp.			8.3
Agropyron repens			1.4
Helianthus annuus			12.7
Fraxinus pennsylvanica			3.9
Solidago canadensis			6.3
Total Species	11	15	17

communities. This also applied to _A. brachyactis_ and _S. occidentalis_ in the short grass and to _H. annuus_ in the wood margin.

Jaccard's Index of Similarity (IS) was applied to express similarity of plant communities in the short grass, tall grass, and edge of woods. This Index expresses the ratio of the common species to all species found in two vegetation segments. Results were: short grass/tall grass 36.8%, short grass/edge of woods 47.4% and tall grass/edge of woods 39.1%. Therefore in giving equal weight to presence and absence of all species, these analyses are not as similar as one would assume on first examination.

For quantitative assessment of the more dominant species, rooted-frequency (Greig-Smith, 1957) was applied. Sociability Index, a means of indicating space relations of individual plants was calculated according to the scale by Braun-Blanquet (1932). Tables 12, 13 and 15 show Cover Values and Sociability Indices for low grass, tall grass and edge of woods. Most species were either socially crowded (group 5) or scattered (group 1). This reflects the pattern of distribution in the population. Mean density and standard error (Tables 12, 13 and 15) also indicate variability of species concentrations in the area. _B. inermis_ and _C. canadensis_ have the highest means. Cover

Table 12. Vegetation data from low grass, July, 1978 (n = 20)

Species	No. Quadrats of Occurrences	Cover	Socia-bility	Relative Frequency %	Relative Density	Relative Dominance	Mean Density ± SE
Bromus inermis	16	2	5	17.2	22.8	24.7	20.9±5.3
Cirsium arvense	17	2	4	18.3	1.9	14.1	1.8±0.4
Calamagrostis canadensis	18	3	5	19.4	66.9	33.3	61.2±9.3
Sonchus asper	11	2	4	11.8	1.7	9.7	1.6±0.5
Parthenocissus quinquefolia	2	R	1	2.2	0.05	0.1	0.1±0.1
Aster brachyactis	14	2	3	15.1	2.8	7.0	2.6±0.5
Rubus idaeus	3	1	1	3.2	0.5	3.1	0.5±0.2
Melilotus alba	2	+	1	2.2	0.4	0.9	0.4±0.2
Artemisia absinthium	2	+	1	2.2	0.6	0.3	0.6±0.4
Aster pansus	1	1	2	1.1	0.8	1.5	0.7±0.7
Symphoricarpus occidentalis	7	2	1	7.5	1.6	5.3	1.5±0.9

Table 13. Vegetation data from Tall grass, July, 1978. (n = 20)

Species	No. Quadrats of Occurrences	Cover	Sociability	Relative Frequency %	Relative Density %	Relative Dominance	Mean Density ± SE
Bromus inermis	20	5	5	31.3	75.9	70.9	80.7±11.3
Calamagrostis canadensis	10	2	5	15.6	18.9	12.3	20.1±5.5
Sonchus asper	10	1	1	15.6	1.2	4.8	1.3±0.3
Cirsium arvense	8	1	2	12.5	0.9	3.7	1.0±0.3
Aster brachyactis	4	1	3	6.3	0.9	1.1	1.0±0.5
Rumex maritimus var *fueginus*	1	1	2	1.6	0.4	1.0	0.4±0.4
Potentilla anserina	1	1	2	1.6	1.2	1.0	1.3±1.3
Polygonum coccineum	2	+	3	3.1	0.1	0.3	0.1±0.1
Symphoricarpus occidentalis	1	+	1	1.6	0.1	0.1	0.1±0.1
Rudbeckia laciniata	1	R	1	1.6	0.05	0.3	0.05±0.05
Mentha arvensis	1	R	1	1.6	0.05	0.1	0.05±0.05
Acer negundo	1	+	1	1.6	0.1	0.3	0.2±0.2
Ribes oxycanthoides	2	+	1	3.1	0.1	0.3	0.1±0.1
Rosa blanda	1	R	1	1.6	0.05	0.1	0.05±0.05
Artemisia absinthium	1	1	1	1.6	0.1	3.8	0.1±0.1

Table 14 . Vegetation data from Edge of Woods, July, 1978. (n = 20)

Species	No. Quadrats of Occurrences	Cover	Socia-bility	Relative Frequency %	Relative Density %	Relative Dominance %	Mean Density ± SE
Bromus inermis	13	3	5	15.3	55.9	43.6	109.0±24.5
Sonchus asper	13	1	1	15.3	0.5	3.9	0.9±0.2
Calamagrostis canadensis	16	3	5	18.8	40.8	30.1	77.1±16.6
Cirsium arvense	11	1	2	12.9	0.6	2.1	1.2±0.3
Rubus idaeus	3	1	1	3.5	0.1	2.1	0.2±0.1
Chenopodium spp.	6	+	3	7.1	0.4	0.8	0.7±0.3
Agropyron repens	1	+	2	1.2	0.1	0.1	0.3±0.3
Helianthus annuus	7	1	1	8.2	0.4	4.1	0.8±0.3
Acer negundo	1	R	1	1.2	0.02	1.2	0.05±0.05
Fraxinus pennsylvanica	2	+	1	2.4	0.08	1.4	0.2±0.1
Rudbeckia laciniata	1	R	1	1.2	0.02	0.05	0.05±0.05
Symphoricarpus occidentalis	2	1	1	2.4	0.2	4.2	0.4±0.3
Aster brachyactis	1	R	1	1.2	0.02	1.2	0.05±0.05
Solidago canadensis	2	1	2	2.4	0.08	3.9	0.5±0.3
Potentilla anserina	1	+	2	1.2	0.1	0.3	0.2±0.2
Melilotus alba	2	+	1	2.4	0.2	0.6	0.4±0.2
Aster pansus	3	+	1	3.5	0.4	0.6	0.8±0.4

Values of these species (Table 10) are also high in these habitats. S. asper had a Cover Value of 65% in the edge of woods the same as B. inermis. I conclude that these species dominated the vegetation in the low grass, tall grass and wood margin.

Results were tested statistically to show the spatial distribution of individuals in the population on sampled plots. The variance : mean ratio was applied and for the t-test the difference between the observed and expected distributions was compared with the standard error. The variance : mean ratio was 381.4 and thus does not conform to a Poisson series with the variance equal to the mean. I conclude that this population was not randomly distributed. The X^2 Goodness of fit test with a mean population of 7.7 from observed number of individual quadrats containing 0, 1, 2 .... $\geq$ 10 B. inermis individuals from population resulted in $X^2 = 1369.1$ and $p < 0.001$. The difference between the Observed and Expected number of occurrences is highly significant and the chances of this difference arising accidentally are much greater than 1000:1.

Increase in variance is an indication of a move towards clumped or non-random distribution and a fall in variance shows that units have a pattern of regular distribution (Kershaw, 1966). This development is relative to the size of the area investigated and the size of the quadrat used. As vegetation is a continum it cannot be classified into discrete entities. Thus in some areas, results showed more than one pattern of distribution. Distribution patterns are important for the distributions of adult *D. variabilis* ticks.

Quantitative vegetation analyses were not made in the mixed herbs and shrubs nor in the woods, but a survey of plant species revealed the following plants: *Sonchus asper*, *Cirsium arvense*, *Rubus idaeus*, *Symphoricarpus albus* (White Snowberry), *Symphorycarpus occidentalis*, *Bromus inermis*, *Calamogrostis canadensis*, *Acer negundo*, *Fraxinus pennsylvanica*, *Quercus macrocarpa*, *Artemisia absinthium*, *Carex assiniboinensis*, *Polygonum coccineum*, *Solidago canadensis*, *Andropogon gerardi*, and *Urtica dioica*.

VII. TICK-VEGETATION INTERACTIONS

(A) Distribution

Distribution of adult *D. variabilis* ticks on vegetation is summarized in Table 15 and 16 . Frequency distribution histogram (Fig. 23) summarizes tick population densities for 1978. The edge of woods area had the highest tick densities. The next highest was tall grass. Mixed

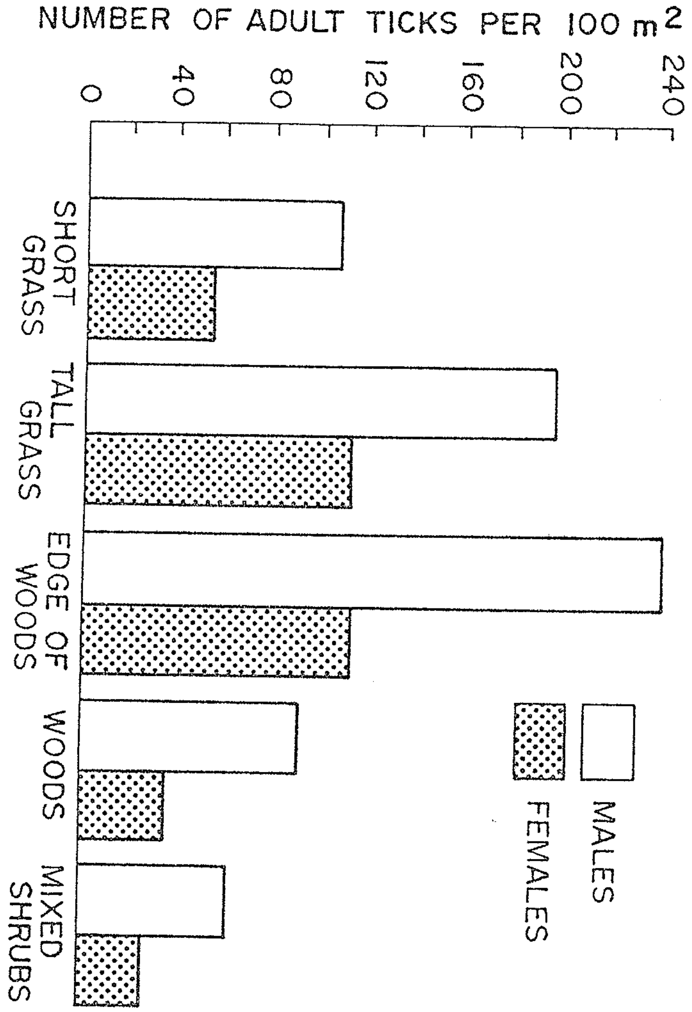
Table 15. Adult _D_. _variabilis_ ticks from vegetation flagging, 1977.

Month		Low Grass	Tall Grass	Edge of Woods	Woods	Mixed Shrubs	Totals	Totals ♀ + ♂
July	♀	2	4	10	3	10	29	49
	♂	3	4	8	1	4	20	
August	♀	-	-	1	-	-	1	1
	♂	-	-	1	-	-	1	
Totals ♀ + ♂		5	8	20	4	14	51	50

Table 16. Adult _D._ _variabilis_ ticks from vegetation flagging, 1978.

Month		Low Grass	Tall Grass	Edge of Woods	Woods	Mixed Shrubs	Totals	Totals ♀ + ♂
May	♀	38	73	86	16	21	234	431
	♂	31	65	66	13	22	197	
June	♀	17	27	36	21	10	111	205
	♂	12	21	37	19	5	94	
July	♀	2	8	8	9	1	28	45
	♂	1	5	5	6	-	17	
August	♀	-	-	2	1	-	4	4
	♂	-	-	-	-	-	-	
Totals	♀	57	108	132	47	33	377	
	♂	44	91	108	38	27	308	
Totals ♀ + ♂		101	199	240	85	59	685	

Figure 23. Number of adult D. *variabilis* ticks on 100 m^2 vegetation, May to August, 1978.


NUMBER OF ADULT TICKS PER 100 m2
0
40
80
120
160
200
240
SHORT GRASS
TALL GRASS
EDGE OF WOODS
WOODS
MIXED SHRUBS
MALES
FEMALES

herbs and shrubs is lowest, with an observed tick population of 60 (Table 16). Although tick densities were low in 1977 (Table 15), the edge of woods had relatively higher numbers of questing adult ticks than the other habitats. The few samples in this area are not sufficient to give a true reflection of the tick populations. Table 17 shows the mean, range and standard error of results for 1978. These results elucidate the tick population densities. The edge of woods has the highest mean for May ($\bar{x} = 30.4$) and June ($\bar{x} = 12.2$) with the tall grass next. In both years of the study, adult ticks were captured from the edge of woods in August and few or none from the other areas. Adult ticks seem to prefer this habitat.

Data from sweeping samples were tested statistically to show distribution patterns of adult ticks. Application of the Poisson distribution with 10 df to the frequency distribution of the number of ticks taken from each vegetation sweeping sample was made. Expected frequencies were given the assumption that ticks were independently and randomly distributed in the vegetation (Poisson distribution). The fit of the observed and expected frequency distribution were tested by a chi-square goodness-of-fit test. Results gave an $X^2 = 59834.3$. Probability of a chi-square this large arising by chance is far smaller than 0.001. I

Table 17. Mean, Range and Standard Error of Adult _D. variabilis_ ticks from vegetation, 1977 and 1978.

	Month	Low Grass		Tall Grass		Edge of Woods		Woods		Mixed Shrubs	
		$\bar{x} \pm$ SE	Range	$\bar{x} \pm$ SE	Range	$\bar{x} \pm$ SE	Range	$\bar{x} \pm$ SE	Range	$\bar{x} \pm$ SE	Range
1977	July	0.8±0.4	0-2	1.3±0.7	0-4	3.0±1.5	0-9	0.7±0.5	0-3	2.3±1.1	0-6
	August	-	0-0	-	0-0	0.3±0.2	0-1	-	0-0	-	0-0
1978	May	11.5±9.6	0-59	23.0±11.6	0-69	30.4±9.7	0-61	4.8±1.8	1-11	7.2±2.2	0-13
	June	4.8±2.5	1-17	8.0±3.2	0-18	12.2±3.4	4-26	6.7±2.6	0-18	2.5±0.2	2-3
	July	0.5±0.3	0-2	2.2±0.9	0-6	2.2±0.7	0-4	2.5±0.8	0-5	0.2±0.2	0-1
	August	-	0-0	-	0-0	0.2±0.1	0-1	0.1±0.1	0-1	0.1±0.1	0-1

conclude that the expected frequencies of the Poisson distribution do not fit the observed frequencies. Consequently ticks were not randomly distributed in the vegetation.

(B) Climatic Effects on Tick Activity

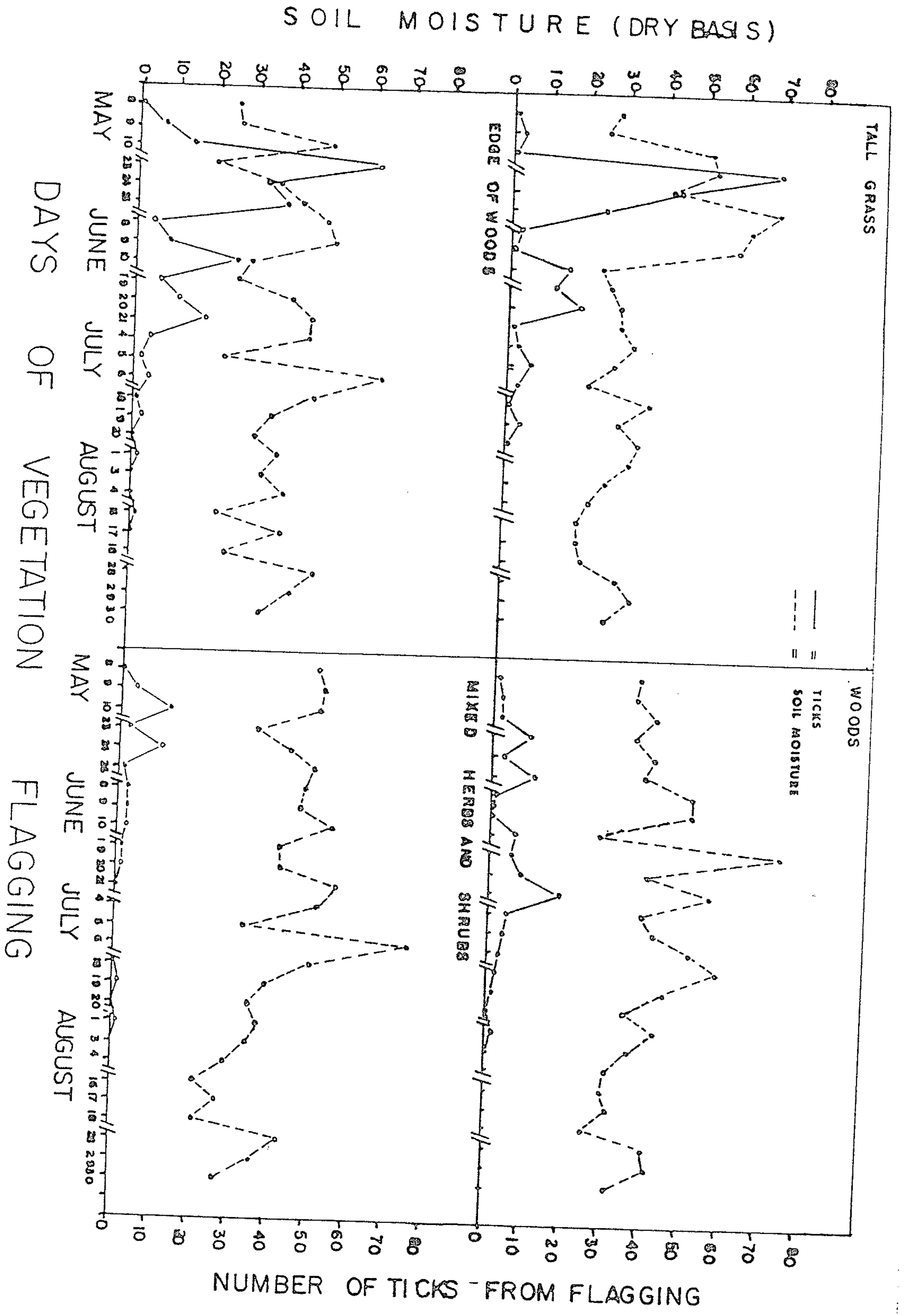
Table 18 shows mean percentage soil moisture (dry basis) for 1978 for each of the five areas and the edge of woods with an overall $\bar{x} = 37.2 \pm 1.9$ (SE) was the area with highest tick densities. Tall grass and low grass are next with 34.9% and 39.0% moisture. Mixed herbs and shrubs and woods have means of 43.2% and 41.8% respectively. It may be concluded from these results that the cyclic dynamics of the adult tick populations in the natural habitat, are influenced by moisture in the ground within ± 32%. Soil moisture greatly affects the soil level microclimate (Milne, 1950). Soil temperature follows average change rather than daily fluctuations of ambient air temperature.

Tick-soil moisture relationship can be seen in Fig. 24. In all five distributions the initial fluctuations of tick and soil moisture are great. Peaks and low points of the two tend to alternate except for only one, the edge of woods. After this initial alternate fluctuation, there

Table 18 . Mean and Standard Error of Soil Moisture (dry basis) for each Vegetation Sampling Month, 1978.

Vegetation	May $\bar{x} \pm$ SE %	June $\bar{x} \pm$ SE %	July $\bar{x} \pm$ SE %	August $\bar{x} \pm$ SE %	Range %
Low Grass	32.8 ± 3.0	38.9 ± 2.8	46.9 ± 4.1	37.2 ± 3.4	23.4 - 60.8
Tall Grass	47.3 ± 7.3	37.3 ± 7.1	30.4 ± 2.6	24.9 ± 1.9	18.5 - 68.5
Edge of Woods	34.6 ± 5.4	39.7 ± 4.1	39.7 ± 5.8	34.9 ± 2.7	19.1 - 62.7
Woods	38.6 ± 1.4	49.8 ± 6.4	44.7 ± 3.4	34.1 ± 2.2	25.2 - 73.8
Mixed Shrubs	46.4 ± 3.2	48.3 ± 2.5	47.3 ± 6.4	30.6 ± 2.5	20.9 - 75.2

Figure 24. Tick-Soil Moisture relationship.


SOIL MOISTURE (DRY BASIS)
TALL GRASS
WOODS
EDGE OF WOODS
MIXED HERBS AND SHRUBS
—— = TICKS
- - - = SOIL MOISTURE
MAY
JUNE
JULY
AUGUST
DAYS OF VEGETATION FLAGGING
NUMBER OF TICKS FROM FLAGGING

seems to be synchronization of the rise and fall until July when the ticks abruptly disappear. At the same time a definite drop occurs in percentage soil moisture, falling to 10-20% by the end of August. Data plotted on these graphs illustrate the relationship between tick activity and moisture in the soil and the soil level microclimate

Mean temperatures from May to August, 1978 were 22.6°C with a range of 8.1°C to 43.5°C. Ticks were captured on the vegetation at these extreme temperatures, but on the average the majority were captured at temperatures ranging from 19°C to 26°C.

Humidity and light did not seem to affect the daily fluctuations nor the densities of ticks during periods of peak activity. In nature, humidity, temperature and to some extent, light, are closely related and their effects on ticks are synchronous rather than isolated.

(C) Densities of Ticks

The following densities, i.e., number of ticks per square metre, were found in the study areas in 1978; namely, edge of woods 0.09, tall grass 0.07, low grass 0.04, woods 0.03 and mixed herbs and shrubs 0.02. Estimation of tick population size was made by application of the Removal Method and by Zippen's Method (Zippen, 1958) (Appendix XI(c). Estimated population size for 1977 was 36,000 adult ticks per hectare, and 148,000 adult ticks per hectare in 1978. There were more ticks in 1978 than in 1977 by a factor of slightly more than 4 to 1.

VIII. HAEMAPHYSALIS LEPORISPALUSTRIS

A. Avian Hosts

Nineteen species of birds represented by 64 specimens were examined for ticks in 1977 (Appendix XIII). Of these, 11 species (48 specimens) were infested with larvae and nymphs of *H. leporispalustris*. In 1978, 61 species represented by 1,727 specimens were examined (Appendix XIII), and 25 species (172 specimens) were infested (Table 19). Five species, *X. xanthocephalus*, *I. galbula*, *H. fuscescens*, *M. ater* and *D. petechia* caught on both the beach ridge and in Oxbow woods in 1978 were infested. The remaining 20 species were found infested on the ridge. Yellow warbler and Tennessee warbler were the most abundant numerically (Table 19).

This study examined 25 summer resident bird species that breed at Delta Marsh; namely, eastern wood pewee, house wren, catbird, brown thrasher, American robin, veery, Tennessee warbler, Nashville warbler, yellow warbler, Myrtle warbler, palm warbler, ovenbird, mourning warbler, yellow-headed blackbird, Canada warbler, American redstart, redwinged blackbird, orchard oriole, Baltimore oriole, brown-headed cowbird, pine siskin, song sparrow, northern waterthrush, clay-coloured sparrow, and blackpoll warbler. There were several non-breeders which were transients of many local breeders and

Table 19. Number of infested birds, habitat, prevalence and intensity, 1978.

Bird Species	No. Caught	No. Infested	Habitat	No. of Ticks	Prevalence (%)	Intensity
C. virens	3	1	T	1	33	1.0
Tro. aedon	12	9	S	18	75	2.0
Du. carolinensis	95	17	S	26	18	1.5
Tox. rufum	1	1	S	86	1	86.6
Tur. migratorius	5	5	S	72	1	14.4
H. fuscescens	17	9	G	25	53	2.8
V. peregrina	381	14	T	66	3.7	4.7
V. ruficapilla	23	3	T	9	13.1	3.0
De. petechia	445	3	S	8	0.7	2.7
De. coronata	13	3	T	3	23.0	1.0
De. striata	16	1	T	4	6.3	4.0
De. palmarum	3	1	T	2	33	2.0
Seiu. aurocapillus	23	3	G	6	13.04	2.0
Seiu. noveboracensis	64	1	G	10	1.5	10.0
O. philadelphia	12	2	S	4	1.6	2.0
W. canadensis	7	2	T	3	28.5	1.5
Seto. ruticilla	56	1	T	3	1.7	3.0
X. xanthocephalus	6	3	M	3	50	1.0
A. phoeniceus	15	8	M	12	53	1.5
I. spurius	1	1	T	1	100	1.0

cont'd

Table 19 cont'd. Number of infested birds, habitat, prevalence and intensity, 1978.

Bird Species	No. Caught	No. Infested	Habitat	No. of Ticks	Prevalence (%)	Intensity
I. galbula	4	3	T	6	75	2.0
Mo. ater	11	11	G	19	100	1.7
Spin. pinus	10	1	T	1	10	1.0
Spiz. pallida	30	28	G	201	93	7.2
Me. melodia	44	41	G	165	93	4.0
	1297	172		754	13.3	4.4

T = Tree; S = Shrub; G = Ground; M = Marsh.

non-breeders, several were infested with H. leporispalustris (Table 20).

Resident or breeder birds have four nest habitats, i.e., tree, shrub, ground and marsh. Of the 14 residents, three nest on the ground (veery, ovenbird and song sparrow), five in shrubs (robins, yellow warblers, whose nests are parasitized by cowbirds and therefore are classified as shrub birds, plus the brown thrasher and catbird); four in trees (pine siskin, baltimore oriole, and orchard orioles and catbird); and two in the marsh (yellow-headed blackbirds and redwinged blackbirds). Only one brown thrasher was examined and it had 82 larval ticks in 1978. The three ground nesting species also contribute to the higher tick count of the resident populations.

Non-resident birds or transients which were infested with ticks included 11 species, six of which are ground nesters (Tennessee, mourning, Nashville, palm and Canada Warblers and ovenbird), three of which are shrub nesters and two tree nesters. All of these birds breed near or north of The Pas, Manitoba, e.g., Churchill.

Table 20. Bird species infestations by *H. leporispalustris* according to breeding area in 1978.

Species	No. Examined	No. Infested	Prevalence (%)	No. of Ticks
Resident:				
C. virens	3	1	33	1
Tro. aedon	12	9	75	18
Cu. carolinensis	95	17	17.9	26
Tox. rufum	1	1	100	86
Tur. migratorius	5	5	100	72
H. fuscescens	17	9	53	25
De. petechia	445	3	0.7	8
X. xanthocephalus	6	3	50	3
A. phoeniceus	15	8	53.3	12
I. spurius	1	1	100	1
I. galbula	34	3	8.8	6
Mo. ater	11	11	100	19
Spin. pinus	10	1	10	1
Me. melodia	44	41	93.2	165
Totals	699	113		443

113 infested birds in 699 examined = 13/699 = 0.0162 = 16.2% prevalence.

113 infested birds had 443 ticks intensity = 443/113 = 3.9 ticks per infested bird.

443 ticks found on 669 birds examined = 0.63 Prevalence X Intensity 16.2 x 3.9 = 62.2

cont'd

Table 20 cont'd. Bird species infestations by *H. leporispalustris* according to breeding area in 1978.

Species	No. Examined	No. Infested	Prevalence (%)	No. of Ticks
Non-Resident:				
V. peregrina	381	14	3.7	66
V. ruficapilla	23	3	21.7	9
De. coronata	13	3	23.1	3
De. striata	16	1	6.3	4
De. palmarum	3	1	33.3	2
Seiu. aurocapillus	23	3	13	6
Seiu. noveboracensis	64	1	1.6	10
O. philadelphia	12	2	16.7	4
W. canadensis	7	2	28.6	3
Seto. ruticilla	56	1	1.8	3
Spiz. pallida	30	28	93.3	165
Totals	628	59		275

59 infested birds in 628 examined = 59/628 = 0.094 = 9.4% prevalence.

59 infested birds had 275 ticks intensity = 275/59 = 4.7 = ticks per infested bird.

275 ticks found on 628 birds examined = 0.44

Prevalence x Intensity = 9.4 x 4.7 = 44.18

B. Prevalence, Intensity and Occurrence

Prevalence for all species for 1977 was 77.1% and 13.1% in 1978. The netting effort was intensified in 1978 and a larger number of birds was thus examined. This accounts for the wide difference in the prevalence results for the two years. Of the individual species, the common grackle, brown-headed cowbird and brown thrasher had the highest prevalence of 100% in 1977. In 1978 prevalence was high in the brown-headed cowbird 100%, American robin 100%, clay-coloured sparrow 93.3% and song sparrow 93.2%.

Intensity for all species was 3.4% in 1977 and 4.4% in 1978. The common grackle was highest with 6.9, American robin next with 5.5 and the brown thrasher 4.6. Intensity was high in 1978 with brown thrasher 86.6 followed by American robin with 14.4 and northern water-thrush 10.0.

Occurrence in all species was 262.2 in 1977 and 56.3 in 1978. Highest among the bird hosts in 1977 was the common grackle (690), American robin (550) and brown thrasher (460). In 1978 occurrence was 8,600 for the brown thrasher, 1,440 for the American robin and 671.8 for clay-coloured sparrow.

Table 20 indicates prevalence for summer resident breeders and non-resident breeders. Fourteen species breeding at Delta Marsh were infested with *H. leporispalustris*.

Prevalence was high for brown thrasher (100%), brown-headed cowbird (100%) and robin (100%).

Birds were classified according to foraging habitats into tree birds, shrub birds and ground birds and tick infestation calculated according to these habitats (Table 21). Intensity was 5.9 for shrub birds, 4.6 for ground birds and 3.0 for tree birds. Fifty percent of the ground birds were infested and fewer of the other habitat species.

C. Seasonal Distribution

Figure 25 shows the distribution of larvae and nymphs in Oxbow woods (May 15th - July 22nd) and in the beach ridge (July 24th - August 31st). There were fewer ticks on birds on the ridge. It is not possible to tell whether the data for the ridge reaches a peak because sampling was not done on this area before July, but the indication is that there were numerically large numbers of larvae and nymphs in July and August.

Table 21. Number of Ticks on Birds from Three Habitats - Delta Marsh - 1978.

No. Caught	No. Infested	Bird Name	Prevalence (%)	No. of Ticks	Intensity
TREE					
3	1	*C. virens*	33	1	1.0
381	14	*V. peregrina*	3.7	66	4.7
23	5	*V. ruficapilla*	21.7	9	1.8
13	3	*De. coronata*	23.1	3	1.0
16	1	*De. striata*	6.3	4	4.0
3	1	*De. palmarum*	33.3	2	2.0
7	2	*W. canadensis*	28.6	3	1.5
57	1	*Seto. ruticilla*	1.8	3	3.0
1	1	*I. spurius*	100	1	1.0
34	3	*I. galbula*	8.8	6	2.0
10	1	*Spin. pinus*	10	1	1.0
548	33	11 species	6.0	99	3.0

33 infested birds in 548 examined = 6.0% prevalence.

33 infested birds had 99 ticks or 3.0 tick/infested bird, intensity.

547 birds had 99 ticks or 0.18 ticks per bird, Prevalence X Intensity = 6.0 x 3.0 = 18

No. Caught	No. Infested	Bird Name	Prevalence (%)	No. of Ticks	Intensity
SHRUBS					
12	9	*Tro. aedon*	75	18	2.0
95	17	*Du. carolinensis*	18	26	1.5
1	1	*Tox. rufum*	100	86	86.0
445	3	*De. petechia*	0.7	8	2.7
12	2	*O. philadelphia*	16.7	4	2.0
5	5	*T. migratorius*	100	72	14.4
570	37	6 species		214	

37 infested birds in 570 examined = 6.5% prevalence.

37 infested birds had 214 ticks or 5.9 tick/infested bird, intensity.

570 birds had 214 ticks or 0.375 ticks per bird, Prevalence X Intensity = 6.5 x 5.9 = 38.35

cont'd

Table 21 cont'd. Number of Ticks on Birds from Three Habitats - Delta Marsh - 1978.

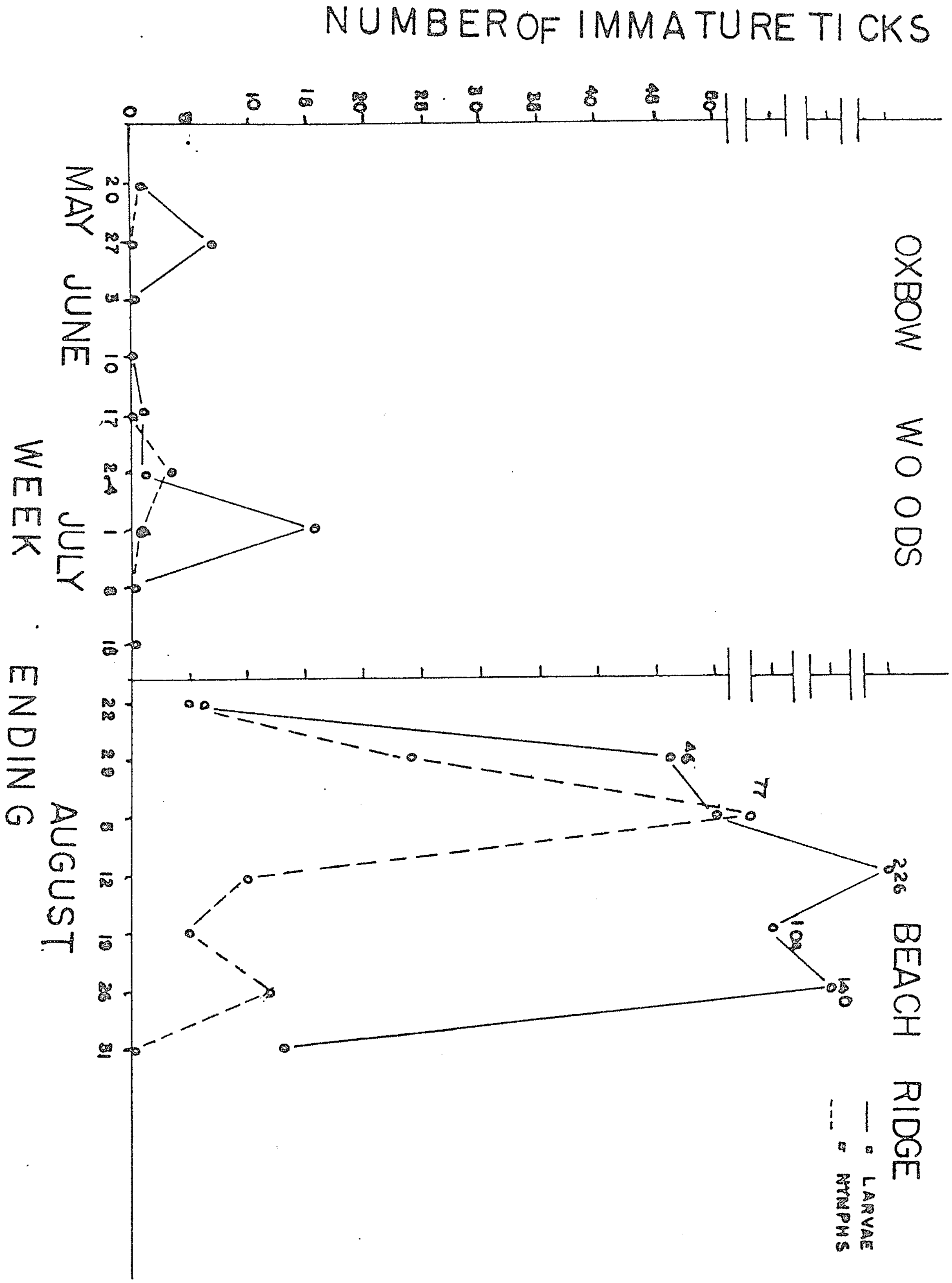
No. Caught	No. Infested	Bird Name	Prevalence (%)	No. of Ticks	Intensity
<u>GROUND</u>					
17	9	<u>H</u>. <u>fuscescens</u>	53	25	2.0
23	3	<u>Seiu</u>. <u>aurocapillus</u>	13	6	2.0
64	1	<u>Seiu</u>. <u>noveboracensis</u>	1.6	10	10.0
30	28	<u>Spiz</u>. <u>pallida</u>	93	201	7.2
44	41	<u>Me</u>. <u>melodia</u>	93	165	4.0
11	11	<u>Molo</u>. <u>ater</u>	100	19	1.7
189	93	6 species		426	

93 infested birds in 189 examined = 46% prevalence.

93 infested birds had 426 ticks or 4.6 ticks/infested bird, intensity.

189 birds had 426 ticks or 2.25 ticks per bird, Prevalence X Intensity = 46 x 4.6 = 211.6

Figure 25. Seasonal variation of _H_. _leporispalustris_ at Oxbow Woods and Delta Beach Ridge, 1978.



NUMBER OF IMMATURE TICKS
0
10
18
20
28
30
40
48
50
OXBOW WOODS
BEACH RIDGE
— ○ LARVAE
-- ○ NYMPHS
20
27
3
10
17
24
1
8
15
22
29
5
12
19
26
31
46
77
226
104
150
MAY
JUNE
JULY
AUGUST
WEEK ENDING

D. Recaptures

Seventeen birds were recaptured within 2-47 days and two other birds were captured a third time. Two catbirds and one song sparrow were not infested the first time on July 27th, 31st and 31st, but upon recapture on August 2nd, 2nd and 13th, had 4, 5, and 12 immatures respectively.

E. Densities

In 1978, 303 birds were caught in nets in Oxbow woods between May 15th and July 22nd and total net hours were 289. Average bird density was 1.1 bird/net hour. From July 24th to August 31st, 1,424 birds were caught in nets on the beach ridge and total net hours were 1,120. Average bird density was 1.3 birds per net hour. These densities are very close.

F. Leporid Hosts

One *Lepus americanus*, one *Sylvilagus floridanus* and one *Lepus townsendii* were caught in 1977. *L. americanus* had 56 larvae, 32 nymphs and 18 adults of *H. leporispalustris*.

S. floridanus had 16 nymph and 14 adult *H. leporispalustris*. *L. townsendii* was not infested. In 1978, four *L. americanus* were examined for ticks. One caught on July 15th had 639 *H. leporispalustris*, the highest collected for the season. Of these, 275 were larvae, 213 nymphs and 151 adults. One *L. americanus* caught on May 19th had 18 larvae and 11 nymphs, and another caught on July 10th had 10 larvae, 8 nymphs and 7 adults. The last *L. americanus* was caught July 26th. It carried 7 adult ticks.

No adult *H. leporispalustris* were found on birds but all three growth stages were found on leporids.

G. Host Records

Eighteen bird species were recorded as new hosts for *H. leporispalustris*. These are; eastern wood pewee, house wren, veery, Tennessee warbler, Nashville warbler, yellow warbler, myrtle warbler, blackpoll warbler, palm warbler, northern waterthrush, mourning warbler, Canada warbler, American redstart, yellow-headed blackbird, orchard oriole, northern oriole, pine siskin and clay-coloured sparrow.

DISCUSSION

The American dog tick *D. variabilis* (adult) actively seeks a host from April to mid-August each year, with a peak in May and June, at Delta Marsh. This activity pattern is controlled by environmental factors and may vary from year to year. As mating occurs on the host the questing ticks, rather than the total adult population, make up the potential breeding population. Therefore seasonal questing activity plays a major role in the regulation of population size. Several studies (Sonenshine, 1972; McEnroe 1975b; Maxwell, *et al.*, 1978 and Garvie, *et al.*, 1978) have elucidated the seasonal activity and host associations of *D. variabilis* and contributed to the understanding of its population dynamics. Nevertheless, important gaps remain in our knowledge of the ecology of these ticks.

I. TICK SPECIES FOUND AT DELTA MARSH

A. *Dermacentor variabilis* (Say)

D. variabilis was the most common species in the study area. It occurred in high densities in open grassland and the edge of woods. The larval stage occurred in greater densities than the nymphal and adult stages.

B. *Haemaphysalis leporispalustris* (Packard)

H. leporispalustris was present in large numbers. It is an ectoparasite of leporids and many bird species. The ticks attacked mainly birds that are ground feeders. The young of several bird species that are not ground feeders were attacked yet their adults seldom were. The young birds probably become infested while learning to fly and probably land more frequently on the ground in their preliminary flight activity. Only larvae and nymphs of *H. leporispalustris* were found on birds but leporids were infested with larvae, nymphs and adults.

C. *Haemaphysalis chordeilis* (Packard)

Only one larva of *H. chordeilis* was found on a Yellow-headed blackbird in the two years of the study. As this isolated specimen was taken from the bird on June 21st, long after the arrival of migrants from the south, the presence of this tick cannot be interpreted to have been carried by a migrating Yellow-headed blackbird. The bird could have picked up the tick in the Delta area or in the neighbourhood. The question that remains unanswered is why there was only one *H. chordeilis*.

D. *Dermacentor albipictus* (Packard)

Kucera (1974), who conducted an ecological study on *Odocoileus virginianus* at Delta Marsh, reported the presence of *D. albipictus* (Winter tick) on these mammals in winter, but as I did not survey ticks in winter, I had no tick specimen to confirm the report.

II. SEASONAL DYNAMICS OF TICKS ON MAMMALS

A. Mammal Population Densities

Host densities and infestation patterns of ticks on hosts can be monitored on the trappable part of the host population. Kikkawa (1964) and Tanton (1965) reported that distinct trappable and untrappable mice and voles exist in populations and that their numbers vary over the year, with voles being less trappable in October and November while mice are less trappable in the summer. A high population of voles were caught in traps in the summer of 1977 and 1978.

From the estimates of the numbers of small rodents, the study area contained a high density of hosts. Banfield (1974) reported the following rodent densities per hectare;

C. gapperi 0.4-11 individuals, M. pennsylvanicus 37-111 in fields and 11-370 in marshes, P. maniculatus 2.4-54 and Z. hudsonius 4.5-29 individuals per hectare. Population estimates of rodents in this study were not made according to species, but all four species were lumped together. The joint estimates fall in the ranges of those of Banfield's records (1974). Rodent population numbers were low at the start of trapping, but rose steadily and reached a peak in July and August, after which they declined. This rise and fall in rodent population numbers was reported by Watts (1970). Delta Marsh provides excellent habitats and favourable conditions for the success of host populations. One may conclude that with high populations of rodents, potential tick populations can be excessively high. Small rodents contribute significantly to the success of ticks in nature providing food for high numbers of immature stages. Comparisons of the seasonal variations of host numbers and tick infestation levels reveal a considerable degree of synchronization in the host-parasite life style. Between May and July when the various growth stages of ticks attained peak activity, rodent populations were beginning to reach a peak in July and August.

Some individuals showed trap aversion and avoided traps while others had become trap-addicted which hindered the use of a grid in population estimates. Evidence for this is seen in the high numbers of recaptured mice and voles, which was approximately fifty percent of those caught for the first time. Such a behaviour could greatly influence the accuracy of population size estimates.

First, observations about habitat preferences in this study lead me to agree with Criddle (1932), Gunderson (1959), Getz (1968), Miller and Getz (1972 and 1973) and M'Closkey and Fieldwick (1975), that *C. gapperi* live in woodland habitats with dense debris cover and high moisture availability. This habitat is suitable for tick larvae. *C. gapperi* was the host most heavily parasitized by larvae in 1978 with 1016 larvae in May, 174 in June and 11 in July with $\bar{X}$: SE = 362.5±223.7. According to Banfield (1974) *C. gapperi* move about a great deal, with a home range as large as 1.44 hectares (3.56 acres). They generally do not construct runways of their own but use those of other species. This behaviour exposes them to high tick infestation levels. Although these voles are most active from sunset to sunrise, they are often about during the daylight hours as well and thus have more opportunity of encountering ticks in vegetation.

Secondly, *P. maniculatus* were found in grassy wooded areas. Such areas are often a little drier than the *C. gapperi* habitats, and are thus a disadvantage for larval success. Thirdly, *M. pennsylvanicus* were usually found in moist upland grasses with dense herbaceous cover (Pearson, 1959; Zimmerman, 1965; Saunderson, 1950). These hosts have larger bodies than the other rodent host species encountered in this study. The positive association of M. pennsylvanicus to deep litter mat reflects the preference of this species for runway construction (M'Closkey and Fieldwick, 1975). M. pennsylvanicus move in grass tunnels and thus have greater chances of encountering ticks. Ticks are less mobile and remain suspended on grass blades waiting for a passing host. Behaviour of hosts such as movement in tunnels and large home range, raise the chance of encounter with ticks and will increase potential parasitization.

In 1977 M. pennsylvanicus had more nymphs than the other rodent species. They had 47 nymphs in June, 60 in July and 13 in August and in 1978 they had 12 in May, 112 in June, 73 in July and 8 in August. Territories of C. gapperi and M. pennsylvanicus are distinct, i.e., they are in wooded areas and in the grassland outside the woods. In this study, there were more larvae on C. gapperi, and therefore in the woods, and there were more nymphs on M. pennsylvanicus, and therefore in the grass. With adult ticks abundant in the edge of woods, tall grass and short grass there seems to be a natural transition trend from woods to open grassland by the different growth stages of D. variabilis.

B. Tick-Host Interactions

D. variabilis is a three-host tick (Appendix IV). The three life stages, larvae, nymphs and adults feed on different hosts. During the course of this study large differences were noted in the degree of utilization of different wild vertebrates as hosts and in the number of simultaneously feeding *D. variabilis* ticks. Mice and voles were the major and intermediate hosts of larvae and nymphs and larger animals such as squirrels, raccoons and skunks were hosts of adult ticks. *D. variabilis* ticks were abundant where rodents and larger mammals shared the same habitat.

D. variabilis larvae and nymphs fed more readily on *C. gapperi* and *M. pennsylvanicus* than on *P. maniculatus* and *Z. hudsonius*. *C. gapperi* and *M. pennsylvanicus*, with fur thicker than that of *P. maniculatus* and *Z. hudsonius*, sustained 78% of the sampled larval and nymphal populations on Grid A in 1977 and 88% in 1978. Both these voles seem to be equally susceptible to larvae and nymphs. In their study in Nova Scotia Garvie, *et al*. (1978) found that *C. gapperi* and *M. pennsylvanicus* in the woody habitat were exposed to fewer subadults than the mice. My results agree with these authors. The grooming behaviour of *P. maniculatus* could account for lower infestation levels in these mice. Similarly, *Z. hudsonius* showed lower levels of infestation than the other major hosts. *Z. hudsonius* move by jumping from one place to another (Jumping Mouse) and this behaviour probably results in less contact with the grass that harbours the ticks. There are several hypotheses which may be postulated to explain these differences and one which is most readily amenable to testing with the data available is that the differences are associated with body sizes of the hosts, i.e., there is a significant relationship between the number of D. variabilis larvae and nymph attaching to hosts, and the body surface area of the host. Miller and Ward (1960) found highly significant correlations between the body weights of pocket gophers and their fleas and lice. I found a similar correlation in rodents with more adults infested and intensity higher than in juveniles.

The level of tick infestation was higher on mature males than on mature females and juveniles. In 1977, 14% of male rodents, 8% females and 6% juveniles were infested with ticks. In 1978 there were 8% males, 7% females and 5% juveniles infested. Males move about more than females during the breeding season while the females spend more time with the litter in burrows. The ratio of males to females in the area was 1.9 : 1.0 in 1978. Thus more males than females were present in the trappable population. The ratio in May, 1978 was ♂ : ♀ = 2.3 : 1.0. Several authors reported that young animals use relatively smaller habitat area than mature animals of the same species. Mohr (1961) considered ectoparasite load as a function of body size of the several hosts rather than host attractiveness. My results agree with those of Miller and Ward (1960) and Mohr (1961) in the importance of body size in relation to tick infestation levels.

In 1977 intensities of ticks on hosts were equal in *C. gapperi* and *Z. hudsonius* and equal in *M. pennsylvanicus* and *P. maniculatus*, but occurrence was highest in *M. pennsylvanicus* and *C. gapperi*. In 1978, intensities were highest in *C. gapperi* and *P. maniculatus* than in *M. pennsylvanicus* and *Z. hudsonius*, and occurrence was high in *C. gapperi* (788) followed by *M. pennsylvanicus* (269), *P. maniculatus* (238) and *Z. hudsonius* (37). Intensity of 10.9 ticks per host in 1978 indicates the high infestation levels not matched in most studies. Garvie, *et al*. (1978) found relative larval density of 3.95 larvae and 3.85 nymphs per host in the spring and June peaks respectively.

Recaptures, once returned to the host populations in the field, continued to provide a reservoir for questing ticks but their role was not unique. In 1977, reinfestation levels were low but increased tremendously in 1978. *C. gapperi* experienced the highest infestation as compared to other hosts. The level of reinfestation on these recaptured hosts compared favourably with that on first catches (Fig. 16). The decline of infestation levels was similar in the first catches and recaptures. *M. pennsylvanicus* and *P. maniculatus* reinfestations were not particularly large.

Spermophilus franklinii were the most abundant larger mammals in the study area. Only adult *D. variabilis* were found on these hosts. Prevalence in 1977 was 27%, and 40% in 1978 and intensity in 1977 and 1978 was 1.0 and 1.6 respectively. Occurrence was 27 and 64 for 1977 and 1978 respectively. Although _S. franklinii_ were not heavily parasitized, they serve as important hosts in the life cycle of _D. variabilis_ in the area. The presence of these hosts in high numbers in the same habitat as mice and voles provides a potential host population for questing larvae, nymphs and adults of _D. variabilis_ ticks, and thus guarantee an undisrupted life cycle each year. _Spermophilus franklinii_ and _Sciurus carolinensis_ are not recorded as hosts for _D. variabilis_ in the literature and are thus recognized as new hosts in this study.

C. Tick Resistance and Disease Transmission

Several studies (Trager, 1939; Roberts, 1968) reported that tick feeding induces resistance to ticks by the host, leading to a decrease in the number of ticks that engorge successfully. Results of recaptured hosts reinfested in this study did not reveal evidence of decline in the feeding population. Riek (1962) and Robert (1968) reported that large numbers of ticks are required to induce acquired resistance. This should lead to a threshold. It is possible that infestation in this study was kept below the threshold. At present, the threshold in _D. variabilis_ is unknown.

It was reported in the two years of this study, that several ground squirrels infected with tularaemia were found in the Winnipeg area. As we have both *D. variabilis* and *H. leporispalustris* in the province and as both are known to transmit tularaemia, there is a remote possibility at present, of these ticks being infected and passing tularaemia to other hosts including man, by transovarial and transstadial transmission.

III. SEASONAL DYNAMICS OF TICKS ON VEGETATION

A. Tick-Vegetation Interactions

High densities of *D. variabilis* adult ticks were found in the wood margin, tall grass and less in the short grass, mixed herbs and shrubs and in the woods. To evaluate the effects of vegetation on the distribution of ticks, quantitative phyto-sociological methods which stressed dominant plant species composition were used. Comparisons were made between tick-capture and plant species density and dominance in the vegetation. Importance Values (IV) (Curtis and McIntosh, 1951) were used to enable the reader to visualize the role of any given species in the community.

Species with high IV's are most conspicuous and contribute more to community structure than those with low IV's, and often give the community its characteristic appearance.

Several plants with high IV's were present in the areas of high tick activity and concentration, i.e., in the edge of woods, tall grass and short grass. Plant species were dominated by *Bromus inermis*, *Calamagrostis canadensis*, *Sonchus asper*, *Aster brachyactis*, *Cirsium arvense* and *Symphoricarpus occidentalis*. These species may play an important part in making the tick environment conducive to questing. Densities of these plants were high and their cover values also high. Cover values provided a better quantitative description of the structure of the plant communities in the three areas of high tick activity. Because of their massiveness, plants such as *Sonchus asper* provided sufficient shelter to the ticks on days of high temperatures, by providing shade to questing ticks and thus reducing tick water loss and soil moisture loss through evaporation. The most important vegetative association for *D. variabilis* was in the edge of woods, where highest capture frequencies occurred. This ecotone represents the first successional stage in forest regeneration and is characterized by a dense understory of numerous saplings. On hot days, the tree canopy at the wood margin provides the necessary shade to keep tick habitats cool but on cool days the wood margin is exposed to the little sunshine that may occur. Moisture levels are also probably maintained at preferable levels at all times.

B. Adult Tick Population Densities

The high densities of ticks at Delta Marsh indicate the suitability of climatic conditions and the availability of hosts in the study area. In 1977 36,000 adult ticks were found per hectare and 148,000 per hectare were found in 1978, a ratio of 1:4. Tick intensity on rodents in 1977 was 3.5 ticks per host and 10.9 ticks per host in 1978, a ratio of 1:3. It is clear from these results that the tick population was greater in 1978 than in 1977. Fluctuations of density changes of this magnitude were reported in other studies by workers in tick populations. Sonenshine (1972) estimated populations of ticks as high as 44,775 and 34,123 ticks per acre (18,578 and 14,158 ticks per hectare) in 1968 and 1969 respectively. In Massachusetts, McEnroe (1975) reported adult population densities at 200 to 1,000 ticks per hectare in the Cape Cod area. Garvie, *et al*. (1978) reported 7,887 to 20,909 ticks per hectare in Nova Scotia in 1974 and 1975. The average for both years was 16,261 ticks per hectare. In Virginia, Sonenshine, *et*. *al*. (1966) reported an estimated adult peak of 1,853 to 5,496 ticks per hectare over a period of three years.

In this study the majority of adult ticks were collected in the edge of woods, tall grass and short grass according to order of decreasing importance. Hall and McKiel (1961) also found more adult ticks in the wood margin and tall grass areas with thick undergrowth. I found high densities of adult ticks along animal trails and footpaths created by humans. Woodland areas with a lot of canopy did not support high populations of adult ticks (Benson, 1964). I observed that ticks were clumped and their localization was sporadic, hence their non-random distribution. Statistical tests confirmed the type of distribution of ticks in the vegetation.

C. Climatic Factors

Delta Marsh has a continental climate with large seasonal fluctuations in temperature and rainfall. The annual difference in temperature during the two years of the study was small compared to seasonal variation. The winter of 1977-78 was colder than that of 1976-77 and the summer warmer. Rainfall varied greatly from month to month but most precipitation occurred in the summer months and though 1978 summer was drier than 1977, no protracted period of drought occurred during the study. The variation in the seasonal adult tick activity is related to the climatological gradient of the area and availability of hosts. Certain climatic phenomena were responsible for initiating and terminating host-seeking activity as well as influencing daily activity.

Ticks emerged in spring when it warmed up and their seasonal activity terminated in autumn when temperatures were above spring temperatures. From these observations one may conclude that temperature alone may not be the most important factor in regulating seasonal behaviour of ticks. It was observed that when temperature was very low on some of the flagging days, fewer ticks were collected. This indicates that tick activity at certain times may be influenced by temperature. At temperatures below 5°C ticks become immobile and show limited activity. Carthy (1958), Wallwork (1960) confirmed that stupor and immobility occur at temperatures below preferred range. McEnroe (1975a) hypothesized that mean winter temperature below 0°C restricted the spread of *D. variabilis* in Massachusetts.

It was observed during the course of this study that high temperatures and low humidities account for absence of questing the next day. Their effects are not immediate but are prolonged. At Delta Marsh, with presence of sufficient moisture and warm evenings, questing continued until early evening on most days. Temperature and humidity are outstanding factors, influencing development. They are important both in their separate and in their combined effects. In nature, these factors operate simultaneously.

Soil level microclimate is another important factor in the life of ticks. As the season progresses from the cold Manitoba winters, the soil warms up and dries out, leaving the soil level microclimate no longer continuously saturated. This could result in ticks being dessicated at ground level as they returned from questing. This could affect variation in tick activity. Conditions within the soil level microclimate regulate initiation as well as termination of activity.

Field data showed no correlation between light and tick density. Ticks were abundant on cloudy days when temperature was not too low and were also found on days when it was not too hot. Light could have an effect at the start and close of another day to signal, together with other parameters, beginning of activity and the end of activity each day. I believe that these factors require further investigation in the laboratory, where they can be dealt with in isolation or as a unit. Some studies have suggested that, rather than light, solar energy is the parameter that has an effect on tick behaviour.

D. Overwintering

There were no *D. variabilis* ticks in the invertebrate samples from winter trapping. Ticks are probably immobile in the winter. This aspect of the study needs further research to establish the position of ticks in winter, so as to complete the picture of their life history.

IV. *DERMACENTOR VARIABILIS* SEASONAL POPULATION DYNAMICS

The start of seasonal activity of *D. variabilis* ticks occurs with increasing temperatures in spring and termination occurs at the end of the summer and beginning of autumn. Tick-host data in this study along with tick development experiments have enabled the determination that *D. variabilis* undergo a two-year life cycle at Delta Marsh.

In the first year of this study there were high densities of adults and larvae of *D. variabilis* in June when when sampling began. Densities of nymphs were lower at this time. In July when the densities of adults and larvae declined, nymphs reached a peak, and by August, populations of all three growth stages had declined tremendously. In the second year, tick activity started in May with exceptionally high larval densities and fairly high densities of adults, but densities of nymphs were relatively low (Tables 8 and 16). In June, adults declined to 48% and larvae to 29%, of the May densities, while nymphs rose nine-fold. There was a further decline of larvae and adults in July while nymphs increased two-fold to reach a seasonal peak. There was a sharp decline in densities of all three stages of development in August (Tables 8 and 16).

This rise and fall of tick densities is indicative of the feeding pattern in the field. Seasonal variation of infestation levels of D. variabilis is a direct product of the course of its cycle of development. By relating the data from laboratory life cycle studies to the pattern of seasonal feeding activity in the field, a model for the course of D. variabilis life history was constructed.

In the first year of the life cycle overwintered adults (Cohort I) successfully engorged on hosts during May and June, will lay eggs which hatch into larvae ± 76 days later, i.e., from July to September. These unfed larvae remain in a dormant state and only become active after the winter. Data of larvae feeding on hosts at Delta Marsh indicate a peak in May and June. Thus larval feeding is unimodal.

In the second year of the life cycle, overwintered larvae start host-seeking in May or earlier if spring was early. Prevailing climatic conditions will determine the beginning of activity. Successfully engorged larvae will moult into nymphs in ±15 days and the latter contributes to the nymphal feeding activity in June and July. Feeding activity is also unimodal and has a peak in July. The engorged nymphs will moult in ±36 days to adults (Cohort II) from late July to

September, depending on temperatures. With lower temperatures, nymphs have been reported to live at least three months without moulting. Adults emerging from moulting nymphs remain dormant and overwinter to start the life cycle again the following spring. Smith, et al. (1946) and Sonenshine (1966) postulated some late season adult activity from nymphal moulting. This did not occur at Delta Marsh in the two years. I conclude that the adult generation from nymphal moulting in July to September, i.e., Cohort II adults, remain dormant and overwinter. Some of the Cohort I and Cohort II adults probably diapause after failing to secure a host and survive to seek hosts again in the following spring and summer, thus extending the life cycle to a possible three years.

The life history pattern outlined, leads me to conclude that the main stages that overwinter are adults (Cohort II) and larvae from the season's Cohort I eggs. There is a possibility that few eggs and nymphs could overwinter but it is not known if they could survive the cold Manitoba winters. Bequaert (1946) reported that under normal conditions, adult, nymphs and larvae have remarkable longevity. It seems that overwinter survival of larvae and adults is an important phenomenon and represents a means of perpetuating the species from year to year.

The seasonal dynamics of the American dog tick at Delta Marsh reveal some interesting similarities and differences when compared with other geographic areas and their climate such as those found in Massachusetts (Smith, et al., 1946; McEnroe, 1974, 1975), Virginia (Sonenshine, 1972) and Nova Scotia (Maxwell, et al., 1978). Several different models have been proposed to explain the adaptations reflected in the different adult activity patterns observed within the range of this tick in North America.

In Massachusetts at the Atlantic Coast (Martha's Vineyard), Smith, et al. (1946) observed a unimodal pattern with seasonal peaks in May or June. McEnroe (1974) described a bimodal pattern at several inland areas of this state. In Virginia, Sonenshine (1972) described a unimodal activity pattern but the seasonal peak was delayed until late June. Warmer spring temperatures facilitate rapid moulting of immatures in this area. Cohort II adults represent the dominant component of the adult population and are responsible for host-seeking activity. In Massachusetts, where temperatures are cooler than in Virginia there prevail Cohort I adults, i.e., they comprise the dominant component of the active populations in most areas. In Delta Marsh, with its severely cold winters, Cohort I adults prevail. In Nova Scotia the pattern of adult tick host-seeking activity consists almost entirely of overwintering, post-diapausing individuals. The questing adults (Cohort I) appear from early April to mid-August. Adults have been collected as late as September. The pattern is unimodal, with peaks at any time between May and late June (Dodds, *et al.*, 1969; Maxwell, *et al.*, 1978). Ticks here apparently have a longer activity season than at Delta Marsh.

Synchronization of life history, vegetation, seasonal climate and host populations has clear advantages to the parasite. First, the greater the number of hosts traversing the tick's habitat, the greater will be the chances of encounters between tick and host, resulting in greater successful parasitization. The large number of hosts available during the tick's major feeding periods will allow tick load to spread more lightly, thus reducing the chance of any effect the host incurred by heavy infestation levels. Second, vegetation cover is necessary to provide shelter from harsh climatic conditions. Thirdly, seasonal climatic factors must be favourable to tick activity from beginning to the end to allow uninterrupted growth and activity. Climatic conditions guarantee development of life cycle without any severe losses in tick population and speeds up development. Delta Marsh seems to be an ideal place for tick development and success with large host populations, plenty of moisture and light, many warm days and uninterrupted vegetation growth. It is thus not surprising that the tick *Dermacentor variabilis* is highly successful in the area and that its population densities are high even though the Delta population is presumably in the northern range of the tick's distribution.

V. HAEMAPHYSALIS LEPORISPALUSTRIS

A. Number and Species of Hosts Examined in 1977 and 1978

Bird trapping in 1977 was not as intensive as it was in 1978. Of the 19 species of birds caught in mist nets, 11 were infested with *H. leporispalustris*. In 1978 61 species were examined and 25 were infested with *H. leporispalustris* and only one species, a yellow-headed blackbird, was infested with one *H. chordeilis* larva. The sampling methods used in 1977 were not suitable for population studies but provided information on the species of ticks and their growth stages, present on birds at Delta Marsh.

In 1978, with an intensified trapping programme, a wide variety of bird species were examined for ticks. Twenty-five species were infested with *H. leporispalustris*. The bird hosts were separated into two categories; first, they were divided according to area of breeding into (a) Resident Breeders and (b) Non-resident Breeders and secondly they were divided according to habitats where they spend most of their active time. These classifications revealed some interesting information as will be shown later. Of all the species infested, brown thrashers had the highest intensity in 1978, followed by ovenbirds and american robin.

B. Resident and Non-resident Breeders

Of the species infested with *H. leporispalustris* at Delta Marsh, 14 species were resident breeders and 11 were non-resident breeders. Six hundred and ninety-nine resident birds had 443 ticks, i.e., 0.63 ticks per bird. Intensity was 3.9 and prevalence 16.2%. Of the non-breeders, 628 birds had 275 ticks, i.e., 0.44 ticks per bird. Intensity was 4.7. There is close similarity in intensity. Prevalence for this group was 0.09, much lower than that for resident breeders (16.2). It is clear from these results that there were more resident birds infested than non-resident. Tick intensity was greater on non-resident birds (417) than on resident birds (3.9) (Table 20).

Comparison of infestations of Tree birds, Shrub birds and Ground birds shows prevalence of 46% for the ground birds, 6.5% for shrub birds and 6.0% for tree birds. The heavily infested ground birds were clay-coloured sparrow and song sparrows. Among the shrub birds the one heavily infested was a brown thrasher that had 86 ticks. Of the tree species Tennessee warbler had highest intensity. Among most of the species which were infested, and which are not ground birds, mainly younger birds were found. These birds were probably undergoing change, leaving their nests and learning to fly and in their moments of failure to fly, would land on the ground and by so doing be exposed to *H. leporispalustris* ticks.

C. Rabbit Hosts of *H. leporispalustris*

High populations of *H. leporisplaustris* were found on rabbits though the rabbit population was not large at Delta Marsh in the two years, the few captured carried high densities of ticks. All three growth stages were found on rabbits. From the high densities on these hosts (650 in an *L. americanus*) it is clear that these ticks use rabbits as their important hosts.

D. Recaptures

Although a few birds were captured more than once, there was no significant level of reinfestation by the ticks and therefore it can be assumed that reinfestation was by chance.

CONCLUSIONS

The variation in the seasonal *D. variabilis* tick activity found at Delta Marsh was related to the population growth of the rodent hosts and to the climatological gradient over the area. Tick activity began in spring when it became warmer. Larvae and adult ticks reached their peak in May and June, and the nymphs in July. Tick activity declined in July and August. Host populations rose steadily and reached a peak in July and August and started to decline by mid-August.

Factors which limit seasonal activity regulate the population size by limiting the reproductive potential of the tick population. The sum of seasonal activity represent the breeding potential of the population. Conclusions about the total populations of both ticks and their hosts must be made very cautiously as it is difficult to assess what fraction of the population is untrappable but data from this study is in substantial agreement with other studies of *D. variabilis* ecology.

The presence of high densities of birds at Delta Marsh is an important factor in the maintenance of the tick *H. leporispalustris* which used bird hosts for its larval and nymphal stages, in addition to its definitive hosts, leporids. Non-resident migrant birds will either introduce more ticks to the area or become infested while stopping over, en route to their nesting sites.

The climatic factors, the availability of hosts and suitable vegetation cover at Delta Marsh provide excellent conditions for the development and population growth of the ticks *D. variabilis* and *H. leporispalustris*.

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APPENDICES

Appendix I. North American Host Records of *Dermacentor variabilis* (Say)

Tick Authority	Host	Larvae	Nymphs	Adults	Locality	Citation
D. variabilis (Say)	Meadow vole (*Microtus pennsylvanicus*)	X	X	X		Bishopp and Trembley, 1945
	Whitefooted Mouse (*Peromyscus leucopus*)	X	X		Montana	Cooley, 1932
	Oldfield mouse (*Peromyscus polionotus*)	X	X		Virginia	Sonenshine, *et al*. 1966
	Deer mouse (*Peromyscus maniculatus*)	X	X		Virginia	Sonenshine, *et al*. 1966
	Meadow Jumping mouse (*Zapus hudsonius*)	X	X			Bishopp and Trembley, 1945
	House mouse (*Mus musculus*	X				Bishopp and Trembley, 1945
	Cotton rat (*Sigmodon* sp.)	X	X		Virginia	Sonenshine, *et al*. 1966
	Norway rat (*Rattus norvegicus*)	X	X			Bishopp and Trembley, 1945
	Rice rat (*Oryzomys palustris*)	X	X			Bishopp and Trembley, 1945
	Baird's mouse (*Perognathus flavus*)	X				Bishopp and Trembley, 1945
	Woodrat (*Neotoma* sp.)		X			Bishopp and Trembley, 1945

cont'd

Appendix I cont'd. North American Host Records of *Dermacentor variabilis* (Say)

Tick Authority	Host	Larvae	Nymphs	Adults	Locality	Citation
D. variabilis (Say)	Pine vole (*Pitymus pinetorum*)	X	X		Virginia	Sonenshine, *et al*. 1966
	Muskrat (*Ondatra zibethica*)	X	X	X		Bishopp and Trembley, 1945
	Raccoon (*Procyon lotor*)		X	X	Montana	Cooley, 1932
	Leopard cat (*Felis pardalis*)			X		Bishopp and Trembley, 1945
	Grey Squirrel (*Sciurus* sp.)	X	X	X		Bishopp and Trembley, 1945
	Red Squirrel (*Tamiasciurus hudsonicus*)		X	X		Bishopp and Trembley, 1945
	Fox Squirrel (*Sciurus apache*)		X		Virginia	Sonenshine, *et al*. 1966
	Southern Flying Squirrel (*Glaucomys volans*)	X			Virginia	Sonenshine, *et al*. 1966
	Eastern harvest mouse (*Reithrodontomys humulis*)	X	X		Virginia	Sonenshine, *et al*. 1966
	Eastern chipmunk (*Tamias striatus*)	X			Virginia	Sonenshine, *et al*. 1966
	Southern bog lemming (*Synaptomys cooperi*)	X	X		Nova Scotia	Dodds, *et al*. 1969
	Weasels (Species unknown)			X	Montana	Cooley, 1932

cont'd

Appendix I cont'd. North American Host Records of *Dermacentor variabilis* (Say)

Tick Authority	Host	Larvae	Nymphs	Adults	Locality	Citation
D. variabilis (Say)	Woodchuk (*mamota monax*)		X			Bishopp and Trembley, 1945
	Starnose mole (*Condylura cristata*)	X				Bishopp and Trembley, 1945
	Shorttail shrew (*Blarina brevicauda*)	X	X		Nova Scotia	Dodds, *et al*. 1969
	Least shrew (*Cryptotis parva*)				Virginia	Sonenshine, *et al*. 1966
	Longtail shrew (*Sorex personatus*)				Nova Scotia	Dodds, *et al*. 1969
	Peccary (*Pecari angulatus*)			X		Bishopp and Trembley, 1945
	Opossum (*Didelphis marsupialis*)		X	X		Bishopp and Trembley, 1945
	Porcupine (*Erethizon dorsatum*)		X	X	Nova Scotia	Dodds, *et al*. 1969
	Skunk (*Mephitis* sp.)			X	Montana	Cooley, 1932
	Fox (*Vulpes* sp.)			X	Montana	Cooley, 1932
	Wolf (*Canis* sp.)			X	Montana	Cooley, 1932
	Badger (*Taxidea taxus*)			X	Montana	Cooley, 1932
	Coyote (*Canis latrans*)			X		Bishopp and Trembley, 1945

cont'd

Appendix I cont'd. North American Host Records of *Dermacentor variabilis* (Say)

Tick Authority	Host	Larvae	Nymphs	Adults	Locality	Citation
D. variabilis (Say)	Wildcat (*Lynx* sp.)			X		Bishopp and Trembley, 1945
	Mountain goat (*Oreamnos americanus*)			X		Bishopp and Trembley, 1945
	Mexican Lion (*Felis hippoletes*)			X		Bishopp and Trembley, 1945
	Mountain Lion (*Felis concolor*)			X	Montana	Cooley, 1932
	Black Bear (*Ursus americanus*)			X	Nova Scotia	Dodds, *et al*. 1969
	Wild hog (*Sus scrofa*)			X	Montana	Cooley, 1932
	Florida Marsh rabbit (*Sylvilagus palustris*)	X	X			Bishopp and Trembley, 1945
	Swamp rabbit (*Lepus aquaticus*)		X		Montana	Cooley, 1932
	Cottontail rabbit (*Sylvilagus* sp.)	X	X	X	Montana	Cooley, 1932
	Blacktailed Jack Rabbit (*Lepus californicus*)	X				Bishopp and Trembley, 1945
	Domestic cat (*Felis domestica*)		X	X		Bishopp and Trembley, 1945
	Domestic dog (*Canis familiaris*)			X	Montana	Cooley, 1932
	Domestic sheep			X	Saskatchewan	Gregson, 1956

cont'd

Appendix I cont'd. North American Host Records of *Dermacentor variabilis* (Say)

Tick Authority	Host	Larvae	Nymphs	Adults	Locality	Citation
D. variabilis (Say)	Cattle			X		Bishopp and Trembley, 1945
	Deer (genus unknown)			X	Montana	Cooley, 1932
	Horse			X	Montana	Cooley, 1932
	Ass			X	Montana	Cooley, 1932
	Mule			X		Bishopp and Trembley, 1945
	Man (*Homo sapien* sp.)			X	Montana	Cooley, 1932

Appendix II . North American Host Records of *Haemaphysalis leporispalustris* (Packard).

Tick, Authority	Host	Larvae	Nymphs	Adults	Locality	Citation
H. leporispalustris (Packard)	Sharp-tailed Grouse (*Pedioectes phasianellus*)	X	X		Nova Scotia	Gregson, 1956
	Spruce Grouse (*Canachites canadensis*)	X			Nova Scotia	Gregson, 1956
	Ruffed Grouse (*Bonasa umbellus*)	X	X	X	Ontario, Nova Scotia	Gregson, 1956
	Ring-necked Pheasant (*Phasianus colchicus*)	X	X	X	Newfoundland	Gregson, 1956
	Domestic Turkey	X	X	X	British Columbia	Gregson, 1956
	Quail (genus unknown)	X	X	X	Montana	Cooley, 1932
	American Robin (*Turdus migratorius*)	X	X		Montana	Cooley, 1932
	Domestic chicken	X	X			Bishopp and Trembley, 1945
	Common Raven (*Corvus corax*)					Gregson, 1956
	Common Crow (*Corvus brachyrhynchos*)	X	X		British Columbia	Gregson, 1956
	Canyon wren (*Catherpes mexicanus*)					Gregson, 1956
	Carolina wren (*Thryothorus ludovicianus*)				Virginia	Sonenshine, *et al.* 1966
	Golden-crowned Sparrow (*Zonotrichia artricapilla*)	X			British Columbia	Gregson, 1956

cont'd

Appendix II cont'd. North American Host Records of *Haemaphysalis leporispalustris* (Packard).

Tick, Authority	Host	Larvae	Nymphs	Adults	Locality	Citation
H. leporispalustris (Packard)	Vesper Sparrow (*Pooecetes gramineus*)		X			Bishopp and Trembley, 1945
	Bachman's Sparrow (*Aimophila aestivalis*)		X			Bishopp and Trembley, 1945
	Chipping Sparrow (*Spizella passerina*)	X	X			Bishopp and Trembley, 1945
	English Sparrow (*Passer domesticus*)	X				Bishopp and Trembley, 1945
	Fox Sparrow (*Passerella iliaca*)		X			Bishopp and Trembley, 1945
	Lincoln Sparrow (*Melospiza lincolnii*)		X			Bishopp and Trembley, 1945
	Savannah Sparrow (*Passerculus sandwichensis*)	X	X			Bishopp and Trembley, 1945
	Song Sparrow (*Melospiza melodia*)	X	X	x		Bishopp and Trembley, 1945
	Swamp Sparrow (*Melospiza georgiana*	X	X			Bishopp and Trembley, 1945
	Tree Sparrow (*Spizella arborea*)	X				Bishopp and Trembley, 1945
	White-crowned Sparrow (*Zonotrichia leucophrys*)	X	X			Bishopp and Trembley, 1945
	Field Sparrow (*Spizella pusilla*)	X	X			Bishopp and Trembley, 1945
	White-throated Sparrow (*Zonotrichia albicollis*)	X	X			Bishopp and Trembley, 1945
	Redstart (*Setophaga* sp.)	X				Bishopp and Trembley, 1945
	Sora Rail (*Porzana carolina*)	X	X			Bishopp and Trembley, 1945

cont'd

Appendix II cont'd. North American Host Records of *Haemaphysalis leporispalustris* (Packard).

Tick, Authority	Host	Larvae	Nymphs	Adults	Locality	Citation
H. leporispalustris (Packard)	Bobwhite Quail (*Colinus virginianus*)	X	X	X		Bishopp and Trembley, 1945
	California Quail (*Lophortyx californicus*)	X	X			Bishopp and Trembley, 1945
	Scaled Quail (*Callipepla squamata*)	X	X			Bishopp and Trembley, 1945
	Yellow-breasted Chat (*Icteria virens*)	X				Bishopp and Trembley, 1945
	Brown-headed Cowbird (*Molothrus ater*)	X	X			Bishopp and Trembley, 1945
	Mourning Dove (*Zenaidura macroura*)		X			Bishopp and Trembley, 1945
	American Goldfinch (*Spinus tristis*)		X			Bishopp and Trembley, 1945
	Bronze Grackle (*Tangarius aeneus*)	X	X			Bishopp and Trembley, 1945
	Purple Grackle (*Quiscalus quiscula*)	X	X			Bishopp and Trembley, 1945
	Ruby-crowned Kinglet (*Regulus calendula*)	X				Bishopp and Trembley, 1945
	Blackbilled Magpie (*Pica pica*)	X	X			Bishopp and Trembley, 1945
	Eastern Meadowlark (*Sturnella magna*)	X	X			Bishopp and Trembley, 1945
	Western Meadowlark (*Sturnella neglecta*)	X	X			Bishopp and Trembley, 1945
	Meadowlark (genus unknown)				Montana	Cooley, 1932
	Horned Lark (*Eremophila alpestris*)	X	X			Bishopp and Trembley, 1945
	Mockingbird (*Mimus polyglottos*)	X				Bishopp and Trembley, 1945

cont'd

Appendix II cont'd. North American Host Records of *Haemaphysalis leporispalustris* (Packard).

Tick, Authority	Host	Larvae	Nymphs	Adults	Locality	Citation
H. leporispalustris (Packard)	Ovenbird (*Seiurus aurocapillus*)	X	X			Bishopp and Trembley, 1945
	Burrowing Owl (*Speotyto cunicularia*)	X	X	X		Bishopp and Trembley, 1945
	Barred Owl (*Strix varia*)		X		Ontario	Gregson, 1956
	Prairie chicken (*Tympanuchus* sp.)	X		X		Bishopp and Trembley, 1945
	Brewer's Blackbird (*Euphagus cyanocephalus*)	X	X		Montana	Cooley, 1932
	Swainson's Thrush (*Hylocichla ustulata*)				Virginia	Sonenshine, *et al*., 1966
	Hermit Thrush (*Hylocichla guttata*)	X	X			Bishopp and Trembley, 1945
	Wood Thrush (*Hylocichla mustelina*)			X		Bishopp and Trembley, 1945
	Brown Thrasher (*Toxostoma rufum*)	X	X			Bishopp and Trembley, 1945
	Sage Thrasher (*Oreoscoptes montanus*)	X				Bishopp and Trembley, 1945
	Blue Jay (*Cyanocitta cristata*)	X	X			Bishopp and Trembley, 1945
	State-coloured Junco (*Junco hyemalis*)	X	X			Bishopp and Trembley, 1945
	Cardinal (*Richmondea cardinalis*)	X	X			Bishopp and Trembley, 1945
	Crissa Thrasher (*Toxostoma dorsale*)		X			Bishopp and Trembley, 1945
	Starling (*Sturnus vulgaris*)	X				Bishopp and Trembley, 1945
	Redwinged blackbird (*Agelaius phoeniceus*)	X	X		Delaware	Peters, 1936

cont'd

Appendix II cont'd. North American Host Records of *Haemaphysalis leporispalustris* (Packard).

Tick, Authority	Host	Larvae	Nymphs	Adults	Locality	Citation
H. leporispalustris (Packard)	Tufted titmouse (*Parus bicolor*)	X	X			Sonenshine, *et al.*, 1966
	Woodpecker (genus unknown)					Gregson, 1956
	Towhee (*Pipilo* sp.)	X	X			Bishopp and Trembley, 1945
	Rufous-sided Towhee (*Pipilo erythrophthalmus*)	X	X			Bishopp and Trembley, 1945
	White-eyed Towhee (*Pipilo e. alleni*)	X	X			Bishopp and Trembley, 1945
	Red-winged Blackbird (*Agelaius phoeniceus*)	X	X			Bishopp and Trembley, 1945
	Blue Bird (*Sialia mexicana*)	X				Bishopp and Trembley, 1945
	Painted Bunting (*Passerina ciris*)	X				Bishopp and Trembley, 1945
	Gray Catbird (*Dumetella carolinensis*)	X	X			Bishopp and Trembley, 1945
	Chaparral Cock (*Geococcyx californianus*)	X	X			Bishopp and Trembley, 1945
	Warbler (genus unknown)		X		Nova Scotia	Gregson, 1956
	Alabama Towhee	X				Bishopp and Trembley, 1945
	Arctic Towhee	X				Bishopp and Trembley, 1945
	Canyon Towhee		X			Bishopp and Trembley, 1945
	Chipmunk (*Eutamias* sp.)					Gregson, 1956
	Pine chipmunk (*Eutamias amoenus*)	X				Bishopp and Trembley, 1945

cont'd

Appendix II cont'd. North American Host Records of *Haemaphysalis leporispalustris* (Packard).

Tick, Authority	Host	Larvae	Nymphs	Adults	Locality	Citation
H. leporispalustris (Packard)	Red squirrel (*Tamiasciurus hudsonicus*)			X	Ontario	Gregson, 1956
	Tree squirrel (*Tamiasciurus* sp.)	X			British Columbia	Gregson, 1956
	Richardson ground squirrel (*Spermophilus richardsonii*)					Gregson, 1956
	Grey squirrel (*Sciurus carolinensis*)	X				Bishopp and Trembley, 1945
	Fox squirrel (*Spermophilus* sp.)		X	X		Bishopp and Trembley, 1945
	Ground squirrel (*Spermophilus* sp.)			X		Bishopp and Trembley, 1945
	Thirteen-lined ground squirrel (*Spermophilus tridecemlineatus*)			X		Bishopp and Trembley, 1945
	Pallid yellow-billed marmot (*Marmota flaviventris*)					Gregson, 1956
	Florida woodrat (*Neotoma micropus*)	X				Bishopp and Trembley, 1945
	Roof rat (*Rattus rattus*)	X				Bishopp and Trembley, 1945
	Fox (*Vulpes* sp. (tick from faeces)		X			Bishopp and Trembley, 1945
	Domestic cat (*Felis domestica*)				Montana	Cooley, 1932
	Man (*Homo sapien* sp.)			X		Gregson, 1956
	Redback vole (*C. gapperi*)	X	X		Nova Scotia	Martell, *et al.* 1968
	Meadow vole (*M. pennsylvanicus*)	X			Nova Scotia	Martell, *et al.* 1968

cont'd

Appendix II cont'd North American Host Records of *Haemaphysalis leporispalustris* (Packard).

Tick, Authority	Host	Larvae	Nymphs	Adults	Locality	Citation
H. leporispalustris (Packard)	Cotton mouse (*Peromyscus nuttalli*)*	X				Bishopp and Trembley, 1945
	(Nest of Northern Golden Mouse)**			X		Bishopp and Trembley, 1945
	Cottontail rabbit (*Sylvilagus* sp.)	X	X	X		Bishopp and Trembley, 1945
	Eastern Cottontail (*Sylvilagus floridanus*	X	X	X		Bishopp and Trembley, 1945
	Mountain Cottontail (*Sylvilagus nuttali*)	X	X	X	Alberta	Gregson, 1956
	European hare (*Lepus europaeus*)		X		Ontario	Gregson, 1956
	Snowshoe hare (*Lepus americanus*)	X	X	X	British Columbia	Gregson, 1956
	White-tailed Jackrabbit (*Lepus townsendii*)	X	X	X	British Columbia	Gregson, 1956
	Mountain goat (*Oreamnos americanus*)	X	X			Bishopp and Trembley, 1945

* Cotton mouse is *Peromyscus gossypinus*

** Golden Mouse is *Ochrotomys nuttalli*

Appendix III. North American Host Records of *Haemaphysalis chordeilis* (Packard)

Tick Authority	Host	Larvae	Nymphs	Adults	Locality	Citation
H. chordeilis (Packard)	Ruffed grouse (*Bonasa umbellus*)	X	X	X		Bishopp and Trembley, 1945
	Spruce grouse (*Canachites canadensis*)	X	X	X	Oregon	Bequaert, 1945
	Sharp-tailed grouse (*Pedioecetes phasianellus*)	X	X	X	South Dakota	McIntosh, 1933
	Turkey (*Meleagris gallopavo*)	X	X	X	Minnesota	Riley, 1941
	Domestic hen		X		Manitoba	Gregson, 1956
	Prairie chicken (*Tympanunchus* sp.)		X		Manitoba	Gregson, 1956
	Ring-necked Pheasant (*Phasianus colchicus*)		X		New Brunswick	Gregson, 1956
	Redwinged Blackbird (*Agelaius phoenicius*)		X			Bishopp and Trembley, 1945
	Marsh hawk (*Circus cyaneus*)		X			Bishopp and Trembley, 1945
	Western Meadowlark (*Sturnella neglecta*)	X	X	X		Bishopp and Trembley, 1945
	Eastern Meadowlark (*Sturnella magna*)	X	X	X		Bishopp and Trembley, 1945
	Quail (species unknown)	X	X			Bishopp and Trembley, 1945

cont'd

Appendix III cont'd. North American Host Records of *Haemaphysalis* *chordeilis* (Packard)

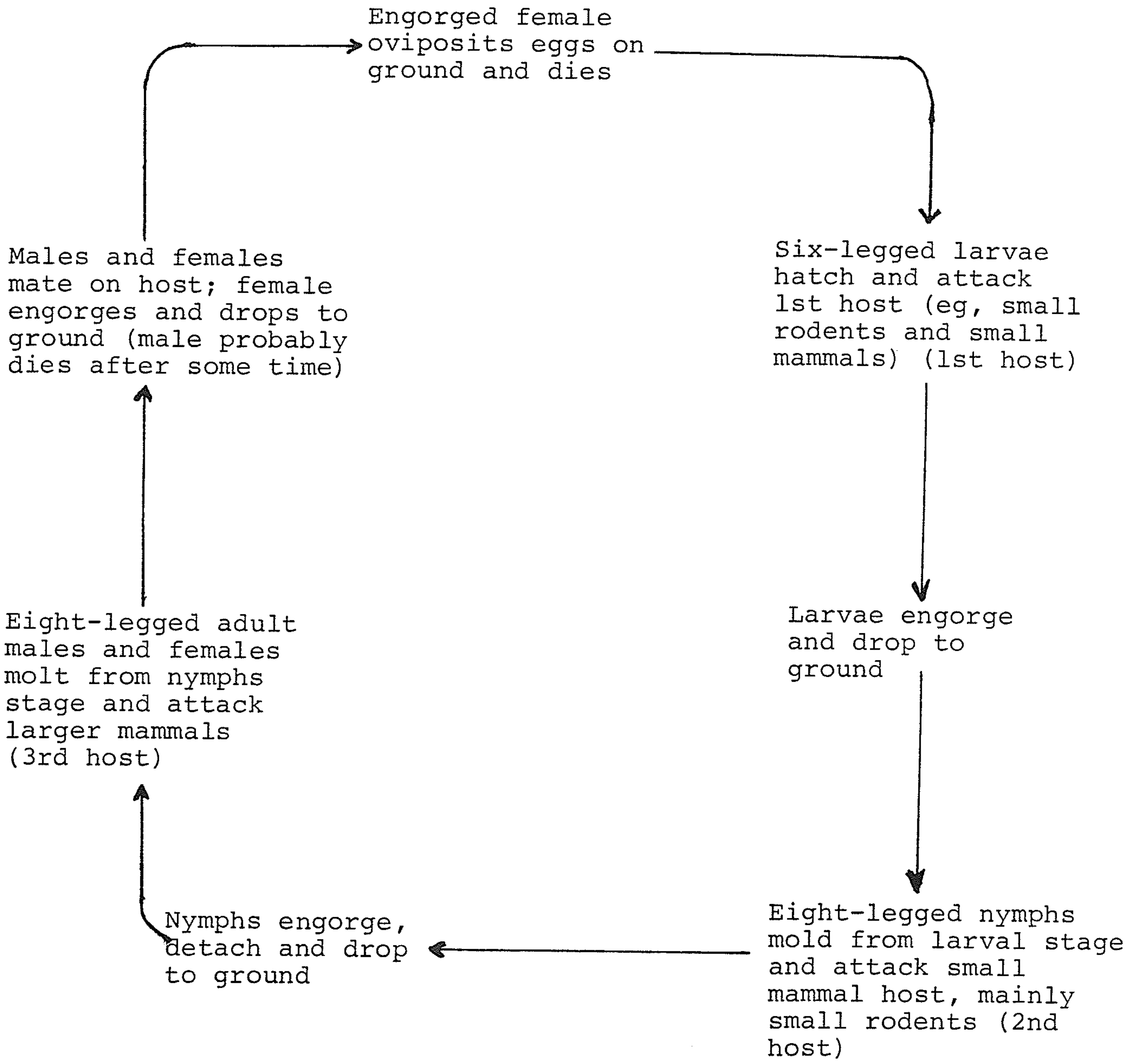
Tick Authority	Host	Larvae	Nymphs	Adults	Locality	Citation
H. chordeilis (Packard)	Florida sparrow (*Ammodramus savannarum*)	X	X			Bishopp and Trembley, 1945
	Savannah sparrow (*Passercullus sandwichensis*)		X			Bishopp and Trembley, 1945
	Wakula Seaside sparrow (*Ammospiza maritima*)		X			Bishopp and Trembley, 1945
	Towhee (*Pipilo* sp.)	X				Bishopp and Trembley, 1945
	Florida wren (*Thryothorus ludovicianus*)	X				Bishopp and Trembley, 1945
	Jackdaw (*Corvus* sp.)	X				Bishopp and Trembley, 1945
	Mountain Sheep (*Ovis canadensis*)			X		Bishopp and Trembley, 1945
	Pallid yellow-billed marmot (*Marmota flaviventris*)			X	British Columbia	Gregson, 1956
	Red Squirrel (*Tamiasciurus hudsonicus*)	X		X	British Columbia	Gregson, 1956
	Tree squirrel (*Tamiasciurus* sp.)					Gregson, 1956
	Man (*Homo sapien* sp.)			X	British Columbia	Gregson, 1956

cont'd

Appendix III cont'd. North American Host Records of *Haemaphysalis chordeilis* (Packard)

Tick Authority		Larvae	Nymphs	Adults	Locality	Citation
H. chordeilis (Packard)	Cattle			X	Saskatchewan	Gregson, 1956
	Cow			X	Washington	Bishopp, 1910
	Horse			X	British Columbia	Gregson, 1956

Appendix IV . Life Cycle of *D. variabilis* (a three host tick).



Appendix V. Weather Records of the University Field Station, Delta Marsh, for 1977, 1978 and part of 1979

Month	Maximum 1* °C	 2* °C	 3* °C	Minimum 1 °C	 2 °C	 3 °C	Mean 1 °C	 2 °C	 3 °C	Precipitation 1 mm	 2 mm	 3 mm	Snow Fall (1977 Only)
January	-15.4	-1.0	-4.5	-25.7	-35.0	-37.5	-20.6	-21.9	-24.2	12.4	17.8	3.6	12.4
February	-5.5	-1.5	-8.0	-16.7	-37.0	-38.5	-11.1	-18.9	-23.9	32.8	9.2	19.2	32.8
March	1.9	7.0	5.5	-9.2	-29.5	-29.0	-3.7	-8.7	-11.7	6.6	8.2	104.5	4.1
April	22.8	18.0	8.5	10.3	-11.0	-29.5	16.6	1.3	-3.5	85.5	23.0	97.4	0
May	13.1	30.0	-	-2.5	-2.5	-	5.3	13.0	-	1.9	103.3	-	0.6
June	21.3	30.0	-	11.9	1.5	-	16.6	16.2	-	85.7	35.5	-	0
July	24.5	30.0	-	12.8	6.5	-	18.7	18.5	-	85.7	21.3	-	0
August	20.3	32.5	-	7.1	1.0	-	13.7	16.5	-	60.1	20.3	-	0
September	17.1	33.0	-	8.1	-1.0	-	12.6	13.5	-	88.4	85.3	-	0
October	14.2	25.5	-	0.7	-7.0	-	7.5	6.5	-	18.7	11.9	-	1
November	0.6	20.0	-	-9.1	-30.5	-	-4.3	-8.2	-	28.7	53.5	-	24.5
December	-13.6	1.0	-	-22.1	-34.0	-	-17.9	-18.3	-	29.1	23.4	-	22.2

*1 - 1977

*2 - 1978

*3 - 1979

Appendix VI. Mammalian hosts data sheet.

Host Data:

Species:

Date of Capture:

Weight:

Body Length:

Tail Length:

Hindfoot Length:

Age:

Sex:

Breeding condition:

Mark on Toes:

Tick Data:

Number on Host:

Location on Host:

Stage of Development:

1. Larvae:
2. Nymphs:
3. Adults:

Species:

Number Attached to Host:

Number Unattached to Host:

Number Engorging:

Number Unengorged:

Trap Number:

Appendix VII. Braun-Blanquet (1932) Scale of Cover and Sociability (Muller-Dombois and Heinz Ellenberg, 1974).

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a) Cover

R = Solitary, with small cover, < 1%

+ = Few, with small cover, < 1%

1 = Numerous but covering < 5%

2 = Covering 5-25%

3 = Covering 25-50%

4 = Covering 50-75%

5 = Covering 75-100%

b) Sociability

1 = Growing in one place, singly

2 = Grouped or tufted

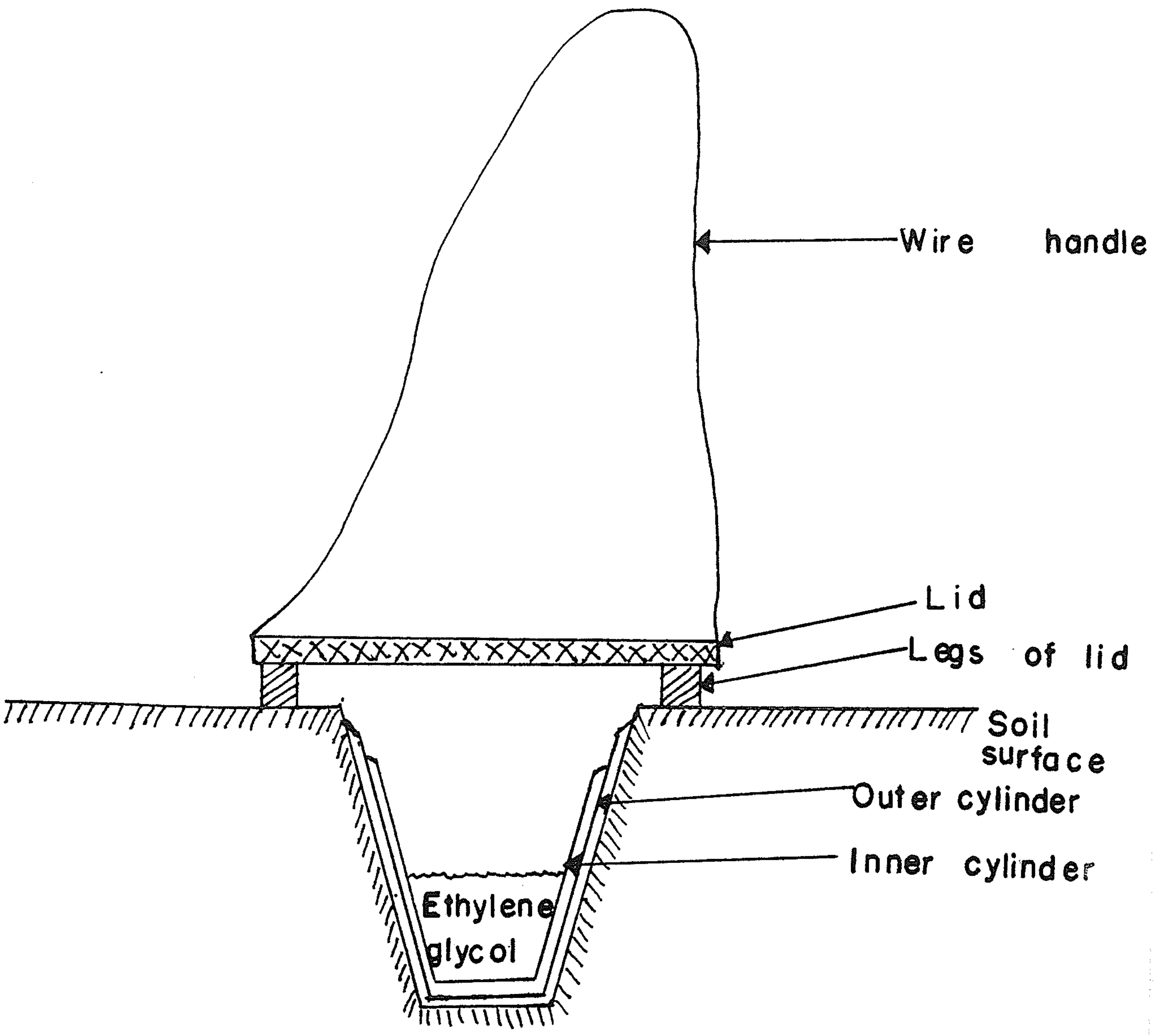
3 = In groups, small patches or cushions

4 = In small colonies, extensive patches or forming carpets

5 = In great crowds (pure populations)

Reference: Braun-Blanquet, J. Plant Sociology. The Study of Plant Communities, 1932.

Appendix VIII. Modified Pitfall Trap.



APPENDIX IX .

Key to family and genera of the ticks _D. variabilis_, _H. leporispalustris_ and _H. chordeilis_.

(From Gregson, 1956).

1 Dorsal scutum present (covering entire dorsum of male and anterior portion of female); Capitulum terminal; integument smooth ...... _Ixodidae_.

2-3 Festoons present (they may not be apparent in engorged specimens); anal groove posterior to anus 4

3-2 Festoons present (they may not be apparent in engorged specimens); anal groove posterior to anus; small ticks 5

4 Ornate ticks; basis capituls and palps of adult together dorsally rectangular in outline (basis capituli triangular in early stage of _D. variabilis_ and _D. andersonii_)................ _Dermacentor_.

5 Inornate ticks; basis capituli and palps together not dorsally rectangular in outline; eyes absent; palps conical, flaring at the base; basis capituli of adult dorsally rectangular, small ticks .... _Haemaphysalis_.

APPENDIX IX cont'd.

Key to Species

1-2 Large ticks; Spurs on Coxa I with facing edges parallel or nearly so; Coxa IV of nymph with no external spur; Spiracular plate with goblet cells, uniformly minute, granular in appearance; Cervical grooves elongate in both sexes and in female closed posteriorly; Nymphs with basis capituli drawn laterally to sharp points; Adults on large hosts; nymphs and larvae on rodents; Found in Saskatchewan east, and in east, central and western U.S. .... variabilis.

2-3 Small ticks; Posterior margin of palpal article 2 noticeably reflexed; hypostome dentition 3/3; Ventral cornua strong and rounded; internal spur of Coxa IV of both sexes small; basis capituli of nymph and larva quadrangular dorsally; common on Cotton-tail and Jack rabbits throughout their range in Canada and the U.S. .... leporispalustris.

3-2 Small ticks; Posterior margin of palpal article 2 only slightly reflexed; hypostome dentition 5/5; Auriculae mild and nearly absent; internal spur of Coxa IV prominent, that of the male being long

APPENDIX IX cont'd.

Key to Species

and pointed; basis capituli of nymph and larva hexagonal dorsally. Found on various ground birds and occasionally on mammals, including man. Distributed widely in Canada and the U.S. .... *chordeilis*.

Appendix X. Taxonomy, Nomenclature and Common Names

TAXONOMY

D. variabilis fits within the genus Dermacentor through its possession of the following characters; a scutum that covers the entire dorsum of male and anterior portion of female; ornamentation and a smooth integument; basis capituli rectangular dorsally and short in relation to its width; basis capituli triangular in larvae and nymphs; eyes present on scutum and usually distinct except for a Mexican species D. dissimilis Cooley; Coxa I to IV increasing progressively in size except in D. reticulatus (Fabricius); suboval or comma-shaped spiracles; festoon on posterior dorsal margin; hypostome spatulate and with three lines of dendicles and an anal groove situated posterior to anus.

Although D. variabilis resembles Dermacentor andersoni (Stiles) closely, the adults are easily recognized by the fine stippled appearance of the goblets in the stigmal plates. In the nymphs the basal spurs of the capitulum are directed backwards, their posterior margins continuing in line with the base line of th- capitulum (Gregson, 1956). In D. andersoni these margins, three in number, form distinct arcs.

H. leporispalustris is easily assigned to the genus Haemaphysalis by the possession of basis capituli, a scutum that covers the entire dorsum of male and anterior of female, inornate body, the presence of festoons, an anal groove posterior to anus, absence of eyes and small size (Gregson, 1956). These characters are also present in *Haemaphysalis chordeilis* (Packard) but males of the latter species have an unusually long coxal spine which separates them from *H. leporispalustris*. In addition, hypostome dentition for *H. leporispalustris* has three rows of teeth whilst *H. chordeilis* has five. Basis capituli of the latter are hexagonal dorsally. (See Appendix IX) for key to the identification of the above ticks).

NOMENCLATURE AND COMMON NAMES

Say (1821) originally described *Ixodes variabilis* and assigned it to the genus *Ixodes*. Subsequently Banks (1908) assigned the species *variabilis* to the genus *Dermacentor* and this combination was accepted (McLeod, 1933; Hearle, 1938; Cooley, 1938; Bequaert, 1946; and Gregson, 1956). This tick is commonly known as the American dog tick. In Manitoba and other parts of North America it is commonly called the wood tick. This name stems from the belief that it occurs in trees, in particular the Oak tree (*Quercus macrocarpa*).

Packard in 1869 assigned *leporispalustris* to the genus *Ixodes*. In 1915 Nuttal, *et al*., transferred the species to the genus *Haemaphysalis*. This combination was accepted by Hearle (1938), Brown (1945), Cooley (1946), Bequaert (1946), Brown and Kohls (1950) and Gregson (1956). In the use of the specific epithet "*leporis-palustris*" I accept Article 32c(i) of the International Code of Zoological Nomenclature and recognize *leporispalustris* as one word. This tick is commonly called the rabbit tick.

Packard (1869) described *Ixodes chordeilis*. Cooley in 1946 assigned this species to *Haemaphysalis*. Prior to that, Newmann described *H. punctata var. cinnabarina* in 1905. In 1915 Nuttall, *et al*., named it *H. cinnabarina*. Likewise Hearle (1938) and Brown (1944) recognized *H. cinnabarina* as a distinct species from *Ixodes chordeilis*. Cooley in 1946, as well as making a new genus assignment, recognized *H. punctata var. cinnabarina* and *H. cinnabarina* as synonyms of *H. chordeilis*. Bequaert (1946), Brown and Kohls (1950) and Gregson (1956) accepted the name *Haemaphysalis chordeilis*. This tick is commonly known as the bird tick.

Appendix XI (a). Lincoln or Peterson Index of Population Estimate of Mark and Recapture

Formula: $x = \frac{an}{r}$

Variance: $x = \frac{a^2 n\ (n-v)}{v^3}$

Where: a = individuals caught first time and marked (Sample 1)

n = individuals caught second time of trapping (Sample 2)

v = individuals in second sample but marked in first sample

x = population estimate size

(b). Simpson's Index of Diversity

$$D = \frac{N\ (N - 1)}{n\ (n-1)}$$

Where: D = Diversity index

N = total number of individuals of all species

n = number of individuals of a species

(c). Zippen's method of population estimate

$$\text{Estimate number in population} = \frac{(Y_1{}^2)}{Y_1 - Y_2}$$

Where: Y_1 = number of first catch

Y_2 = number of second catch

Appendix XII . Jolly's Stochastic Multiple-Recapture Method.

λ = number of samples

N_i = total number of individuals in the population when the ith sample is taken.

n_i = number of individuals in the ith sample.

M_i = total number of marked animals in the population at time i.

m_i = number of marked animals in the ith sample.

S_i = number of individuals released from the 8th sample after marking; not all individuals need be released.

ϕ_i = probability that an individual alive at the moment of release of the ith sample will survive until the time of capture of the (i + 1)st sample, including emigration and death.

B_i = number of new animals joining the population in the interval between the ith and (i + 1)th samples and alive at time i + 1; B_o is defined as equal to N_1.

n_{ij} = number of individuals in the ith sample last captured in the jth sample ($1 \leq j \leq i - 1$)

n_{io} = number of unmarked animals in the ith sample.

αi = m_i/n_i

a_{ij} = $\sum_{k=1}^{j} n_{ik}$ = number of individuals in the ith sample last caught in the jth sample or before.

Z_i = $\sum_{k=i+1}^{\lambda} a_{k,\ i-1}$ = marked individuals before time i which are not caught in the ith sample but are caught subsequently.

R_i = $\sum_{k=i+1}^{\lambda} n_{ki}$ = number of S_i individuals released from the ith sample that are caught subsequently.

$N_{i(j)}$ = expected number in population at time i which first formed the population between times j and j + 1, that is, those, which are members of B_j ($1 \leq j \leq i - 1$); by definition $N_i (i - 1) = B_i - 1$.

Three series of Parameters to be estimated are N_i, ϕ_i and B_i, each of which can change in value over sampling period. In addition the model allows for stochastic fluctuation in the values of N_i and ϕ_i, in the sense that the values of N_i and ϕ_i at any time are effected by stochastic fluctuations apart from variance due to errors in estimating these two parameters.

The population size at time period i is estimated from:

$$\hat{N}_i = \frac{M_i}{\alpha_i} \qquad (i = 1, 2, 3, ---- \ell - 1)$$

Where M_i is

$$M_i = \frac{Si\ Zi}{Ri} + M_i \quad (i = 2, 3, ----- \ell - 1)$$

and $$\alpha_i = \frac{m_i}{n_i} \quad (i = 2, 3, ----- \ell)$$

and the estimate ϕ is

$$\phi_i = \frac{M_i + 1}{M_i - m_i + Si} \qquad (i = 2, 3, ------- \ell - 2)$$

and estimate of B_i is

$$\hat{B} = \hat{N}_i + 1 - \phi (N_i - n_i + si) \quad (i = 2, 3, ------ \ell - 2)$$

The variances of these three estimates are

$$\mathrm{Var}(\hat{N}_i)=\hat{N}_i(\hat{N}_i-n_i)\left[\left(\frac{M_i-m_i+S_i}{M_i}\right)\left(\frac{1}{R_i}-\frac{1}{S_i}\right)+\frac{1-\alpha_i}{m_i}\right]+\hat{N}_i-\sum_{j=0}^{i=1}\frac{N_1^2(j)}{B_i}$$

$$\mathrm{Var}(\phi_i)=\phi_i^{2}\left[\left(\frac{(M_i+1-m_i+1)(M_i+1-m_i+1+S_i+1)}{M_i^{2}+1}\right)\left(\frac{1}{R_i+1}-\frac{1}{S_i+1}\right)\right.$$

$$\left.+\left(\frac{M_i-m}{M_i-m_i+S_i}\right)\left(\frac{1}{R_i}-\frac{1}{S_i}\right)\right]+\frac{1-\hat{\phi}_i}{M_i+1}$$

$$\mathrm{Var}(\hat{B}_i)=\left[\frac{\hat{B}_i^{2}(M_i+1-m_i+1)(M_i+1-m_i+1+S_i+1)}{M_i^{2}+1}\right]\left[\frac{1}{B_i}-\frac{1}{S_i+1}\right]$$

$$+\left[\frac{M_i-m_i}{M_i-m_i+S_i}\right]\left[\frac{\hat{\phi}_i\,S_i\,(1-\;_i)}{i}\right]^{2}\left[\frac{1}{R_i}-\frac{1}{S_i}\right]$$

$$+\frac{(\hat{N}_i-n_i)(\hat{N}_i+1-\hat{B}_i)(1-\alpha_i)(1-\hat{\phi}_i)}{M_i-m_i+S_i}$$

$$+\left[\hat{N}_i+1\;(\hat{N}_i+1-n+1)\right]\left[\frac{1-\alpha_i+1}{m_i+1}\right]+\hat{\phi}_i^{2}\,\hat{N}_i(\hat{N}_i-n\left[\frac{1-\alpha_i}{m_i}\right]$$

The variance estimates are complex but straight forward, the only computational difficulty being the summation term in the variance estimate of N_i, that is, values of $\hat{N}_i(i)$. For two successive samples

$$N_i\ (j=i-1)=\hat{B}_j \tag{11.5}$$

but for two non continuous samples

$$N_k+1\ (j) = \frac{\hat{N}_k + 1 - \hat{B}_k}{\hat{N}_k}\ N_k(j) \qquad K > j \qquad 11.6$$

Where k represents those values of i removed by more than one interval of time from j. Equation (11.6) is a recurrence relation; for example, $N_{5(3)}$ is found as

$$N_{5(3)} = \frac{N_5 - B_4}{N_5}\ N_{4(3)}$$

Where $N_{4(3)}$ is found from E_q (11.5). The term $N_{6(3)}$ can then be found by using $N_{5(3)}$ as $N_k(j)$.

The estimated variances of $\hat{N}_i$ and $\hat{\phi}_i$ are due both to stochastic fluctuations and to errors in the estimation of the parameters. The variances in the population sizes due to errors of parameter estimation are

$$\mathrm{Var}(\hat{n}_i/N_i) = \hat{N}_i(N_i - n_i)\left[\left(\frac{M_i - m_i + S_i}{M_i}\right)\left(\frac{1}{R_i} - \frac{1}{S_i}\right) + \frac{1 - \alpha i}{m_i}\right]$$

and similarly the variances due to errors of estimation for $\hat{\phi}_i$ are

$$\mathrm{Var}\ (\hat{\phi}_i/\phi_i) = \mathrm{Var}\ (\hat{\phi}_i) - \left[\frac{\phi_i^2\ (1-\phi_i^2)}{M_i+1}\right]$$

The standard errors of the estimates are the square roots of these quantities. The remaining variance after the variance due to errors of estimation is subtracted is the variance of the stochastic fluctuations of N_i and ϕ_i. The variance estimate of $\hat{B}_i$ is due entirely to errors of estimation.

Appendix XIII. Common and Scientific Names of Bird Species Examined for Ticks at Delta Marsh in 1977 and 1978.

Common Name		Scientific Name
	Ord.	Cuculiformes
	Fam.	Cuculidae
Black-billed Cuckoo		*Coccyzus erythropthalmus* (Wilson)
	Ord.	Piciformes
Hairy Woodpecker		*Dendrocopos villosus*
Downy Woodpecker		*Dendrocopus pubesceus*
	Ord.	Passeriformis
	Fam.	Tyrannidae
Eastern Kingbird		*Tyrannus tyrannus* (L.)
Western Kingbird		*Tyrannus verticalis* Say
Eastern phoebe		*Sayornis phoebe* (Latham)
Yellow-bellied Flycatcher		*Empidonax flaviventris* (Baird and Baird)
Least Flycatcher		*Empidonax minimus* (Baird and Biard)
Eastern Wood Pewee		*Contopus virens* (L.)
	Fam.	Hirundinidae
Tree Swallow		*Iridoprocne bicolor* (Vieillot)
Bank Swallow		*Riparia riparia* (L.)
Rough-winged Swallow		*Stelgidopteryx ruficollis* (Vieillot)
Barn Swallow		*Hirundo rustica* L.
	Fam.	Sittidae
White-breasted Nuthatch		*Sitta carolinensis* Latham
	Fam.	Troglodytidae
House wren		*Troglodytes aedon* Vieillot
Long-billed Marsh wren		*Telmatodytes palustris* (Wilson)
	Fam.	Mimidae
Catbird		*Dumetella carolinensis* L.
Brown Thrasher		*Toxostoma rufum* L.

cont'd

Appendix XIII cont'd. Common and Scientific Names of Bird Species Examined for Ticks at Delta Marsh in 1977 and 1978.

Common Name	Scientific Name
	Fam. Turdidae
Robin	*Turdus migratorius* (L.)
Swainson's Thrush	*Hylocichla ustulata* (Nuttal)
Veery	*Hylocichla fuscescens* (Stephens)
	Fam. Bombycillidae
Cedar Waxwing	*Bombycilla cedrorum* (Vieillot)
	Fam. Vireonidae
Yellow-throated Vireo	*Vireo flavifrons* Vieillot
Solitary Vireo	*Vireo solitarius* (Wilson)
Red-eyed Vireo	*Vireo olivaceus* (L.)
Philadelphia Vireo	*Vireo philadelphicus* (Cassin)
Warbling Vireo	*Vireo gilvus* (Vieillot)
	Fam. Parulidae
Black and White Warbler	*Mniotilta varia* (L.)
Tennessee Warbler	*Vermivora peregrina* (Wilson)
Nashville Warbler	*Vermivora ruficapilla* Vieillot
Yellow Warbler	*Dendroica petechia* (L.)
Magnolia Warbler	*Dendroica magnolia* (Wilson)
Cape May Warbler	*Dendroica tigrina* (Gmelin)
Myrtle Wwrbler	*Dendroica coronata* (L.)
Black-throated Warbler	*Dendroica virens* (Gmelin)
Blackburnian Warbler	*Dendroica fusca* (Müller)
Chestnut-sided Warbler	*Dendroica pensylvanica* (L.)
Blackpoll Warbler	*Dendroica striata* (Forester)
Palm Warbler	*Dendroica palmarum* (Gmelin)
Ovenbird	*Seiurus aurocapilla* (L.)

cont'd

Appendix XIII cont'd. Common and Scientific Names of Bird Species Examined for Ticks at Delta Marsh in 1977 and 1978.

Common Name	Scientific Name
Northern Water thrush	<u>Seiurus</u> <u>noveboracensis</u> (Gmelin)
Connecticut Warbler	<u>Oporornis</u> <u>agilis</u> (Wilson)
Mourning Warbler	<u>Oporornis</u> <u>philadelphia</u> (Wilson)
Common Yellow throat	<u>Geothlypis</u> <u>trichas</u> (L.)
Wilson's Warbler	<u>Wilsonia</u> <u>pusilla</u> (Wilson)
Canada Warbler	<u>Wilsonia</u> <u>canadensis</u> (L.)
American Redstart	<u>Setophaga</u> <u>ruticilla</u> (L.)
	Fam. Ploecidae
House Sparrow	<u>Passer</u> <u>domesticus</u> (L.)
	Fam. Icteridae
Yellow-headed Blackbird	<u>Xanthocephalus</u> <u>xanthocephalus</u> Bonaparte
Red-winged Blackbird	<u>Agelaius</u> <u>phoeniceus</u> (L.)
Orchard Oriole	<u>Icterus</u> <u>spurius</u> (L.)
Northern Oriole	<u>Icterus</u> <u>galbula</u> (L.)
Common grackle	<u>Quiscalus</u> <u>quiscula</u> (L.)
Brown-headed Cowbird	<u>Molothrus</u> <u>ater</u> (Boddaert)
	Fam. Fringillidae
Rose-breasted Grosbeak	<u>Pheuciticus</u> <u>ludovicianus</u> (L.)
Purple finch	<u>Carpodacus</u> <u>purpureus</u> (Gmelin)
Pine Siskin	<u>Spinus</u> <u>pinus</u> Wilson
American gold finsh	<u>Spinus</u> <u>tristis</u> (L.)
Chipping sparrow	<u>Spizella</u> <u>passerina</u> (Bechstein)
Clay-coloured Sparrow	<u>Spizella</u> <u>pallida</u> (Swanson)
White-crowned Sparrow	<u>Zonotrichia</u> <u>albicollus</u> (Gmelin)
White-throated Sparrow	<u>Zonotrichia</u> <u>leucophrys</u> (Forester)
Song Sparrow	<u>Melospiza</u> <u>melodia</u> (Wilson)

Appendix XIV . Common and Scientific Names of Mammals Caught in Traps in 1977 and 1978

Common Name	Scientific Name
Redback Vole	Clethrionomys gapperi
Meadow Vole	Microtus pennsylvanicus
Deer Mouse	Peromyscus maniculatus
Meadow Jumping Mouse	Zapus hudsonius
Norway rat	Rattus norvegicus
House mouse	Mus musculus
Snowshoe Hare	Lepus americanus
White-tailed Jackrabbit	Lepus townsendii
Eastern Cottontail	Sylvilagus floridanus
American Red Squirrel	Tamiasciurus hudsonicus
Richardson Ground Squirrel	Spermophilus richardsonii
Franklin Ground Squirrel	Spermophilus franklinii
Thirteen-lined Ground Squirrel	Spermophilus tridecemlineatus
Grey Squirrel	Sciurus carolinensis
Masked Shrew	Sorex cinereus
Least Chipmunk	Eutamius minimus
Red Bat	Lasiurus borealis
White-tailed Deer	Odocoileus virginianus
Stripped Skunk	Mephitis mephitis
Raccoon	Procyon lotor
Shorttail Weasel	Mustela erminea
Longtail Weasel	Mustela frenata

Appendix XV . Common and Scientific Names of Plant Species in Grid A - 1978.

Common Name	Scientific Name
Brome grass	*Bromus inermis*
Blue Joint grass	*Calamagrostis canadensis*
Spiny-leaved sow thistle	*Sonchus asper*
Aster	*Aster brachyactis*
Golden dock	*Rumex maritimus* Var *fueginus*
Silverweed	*Potentilla anserina*
Smart weed	*Polygonum coccineum*
Wolfberry	*Symphoricarpus occidentalis*
Green-headed cone flower	*Rudbeckia laciniata*
Mint	*Mentha arvensis*
Manitoba maple	*Acer negundo*
Canada gooseberry	*Ribes oxycanthoides*
Wildrose	*Rosa blanda*
Wormwood Sage	*Artemisia absinthium*
Canada Thistle	*Cirsium arvense*
Virginia creeper	*Parthenocissus quinquefolia*
Wild raspberry	*Rubus idaeus*
Sweet clove	*Melilotus alba*
Many-flowered Aster	*Aster pansus*
Pigweed	*Chenopodium* spp.
Couch grass	*Agropyron repens*
Common sunflower	*Helianthus annuus*
Green Ash	*Fraxinus pennsylvanica*
Golden rod	*Solidago canadensis*

Appendix XVI. Classification

Phylum : Arthropoda
Class : Arachnida
Order : Acarina
Sub Order : Ixodides
Family : Ixodidae
Genus : (i) *Dermacentor*
(ii) *Haemaphysalis*
Species : (i) *D. variabilis*
(ii) *H. leporispalustris*