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WINTER TICK (*DERMACENTOR ALBIPICTUS*) ECOLOGY AND TRANSMISSION IN ELK ISLAND NATIONAL PARK, ALBERTA

BY

OSCAR I. AALANGDONG

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of **MASTER OF SCIENCE**.

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA
SPRING 1994

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22 April 1994

UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled WINTER TICK (*DERMACENTOR ALBIPICTUS*) ECOLOGY AND TRANSMISSION IN ELK ISLAND NATIONAL PARK, ALBERTA submitted by Oscar I. Aalangdong in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE.

Dr. W. M. Samuel

Dr. J. O. Murie

Dr. R. J. Hudson

Dr. M. Belosevic

Date: 7 April 1994

DEDICATION

This thesis is dedicated to Most Reverend Joseph MacNeil, Archbishop of Edmonton, in appreciation of the kind act which paved the way to this achievement.
"Blessed are the merciful, for they shall obtain mercy." (Mt. 5.7).

ABSTRACT

Various aspects of winter tick, *Dermacentor albipictus*, ecology were studied in Elk Island National Park (EINP). The distribution, abundance and density of winter tick larvae were studied in eight habitat types during the autumn of 1991 and 1992. A white flannel, attached to a dowel, was dragged on vegetation along 25 m units at predetermined locations along 2 km transects weekly at four sites in EINP to collect tick larvae. Differences in distribution and abundance of larvae among habitat types were significant being higher in closed aspen forest, open aspen forest, shrubland and labrador tea. Significant differences in distribution and abundance of larvae were observed among sites but not between sites of high and low moose density. Larval abundance peaked in October. Larval density differed among habitat types but not among sites nor between 1991 and 1992.

Questing behavior, height distribution and orientation of tick larvae on vegetation during autumn of 1992 were correlated with weather factors. Larvae responded faster to human breath at high than at low ambient temperatures. Also, questing behavior slowed with age; *i.e.*, as the transmission season progressed. Peak period of larval tick activity was observed between mid September and mid October. Orientation of larvae on vegetation was strongly influenced by wind direction and intensity. They aggregated on the leeward side of vegetation. Heights of larval clumps on vegetation appeared to correspond with the heights of host species in the Park.

Engorged female ticks placed in eight habitat types were observed at various time intervals to record survival and oviposition of females, eclosion of eggs, and longevity of larvae. None of the female ticks placed in sedge bog survived. More female ticks survived and laid eggs in 'closed' than in 'open' habitats. However, reproductive efficiency was higher in the 'open' than in 'closed' habitats. Mean monthly temperatures during tick reproductive period were much lower, with corresponding high relative humidities, in 'closed' than in 'open' habitats. Preoviposition period was generally shorter in 'open' than in 'closed' habitats. Number of eggs laid did not differ significantly among habitats. Incubation period was generally longer in the 'open' than in 'closed' habitats. More eggs hatched and percent eclosion was higher in 'open' than in 'closed' habitats. Larvae also lived longer in 'open' than in 'closed' habitats.

The significance and application of the results of this study to the transmission and managemnent of winter tick in EINP respectively, are discussed.

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I would like to thank my supervisor, Dr. W.M. Samuel for the guidance during my research and writing of this thesis. I am also grateful for his personal interest in and for facilities provided for my career development. I would also like to thank my committee members, Drs. J.O. Murie, and R.J. Hudson, for useful criticisms and helpful suggestions during collection of data in the field. Dr. A.W. Shostak was especially helpful during initial stages of the study and during analysis of the data. Dr. J.C. Holmes inspired me during the course of this program.

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I thank Christiana, my wife, for her support, and assisting me in counting ticks in the laboratory and collecting data in the field. Thanks to my children: Edmund, Patrick and Rosemond, for perservering our long absence. I am very grateful to John and Scholarstica Taabavi, Felix and Adiza Tierekuu , in Ghana, who took care of the children.

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CHAPTER ONE

INTRODUCTION

Introduction

Transmission of parasites from host to host is essential for survival. The ability to find and parasitize hosts is a crucial problem for all parasites because both parasite and host must co-exist in time and space for transmission to take place. Further, success of transmission depends on the abiotic component of, and biotic component in, the habitat in which the parasite and host live. Abiotic component includes physiography of the habitat, light, temperature and moisture. These physical factors of the habitat can affect transmission by altering distribution and survival of host and parasite. They also affect the activity patterns of the parasite that determine the likelihood of host encounter (Granzer and Haas 1991, Sousa and Grosholz 1991). The biotic component, which includes reproduction, survival, activity patterns, densities and distributions of both parasite and host, has direct influence on the success of transmission of parasites to hosts.

Not all habitat types provide the abiotic and biotic conditions necessary for the completion of a particular parasite's life cycle and host's resource needs. Only certain habitat types with a combination of structural features provide optimum conditions for maintenance of parasite and host. Therefore, habitat structure is important in influencing the distribution and abundance of the parasite and, similarly, the distribution and abundance of the host.

Many authors (Semtner and Hair 1973a, b, Mount 1981, Schaalje and Wilkinson 1985, Garris et al. 1990, Kralka and Samuel 1990, Robb and Samuel 1990, Adler et al. 1992) have shown the importance of habitat structure in affecting the distribution and abundance of parasites and consequently its influence on transmission of parasites. Habitat structure can also influence the dynamics and maintenance of parasites within a host population (Carey et al. 1980, see review by Sousa and Grosholz 1991). Transmission of a parasite may be influenced by broad to narrow dimensions of habitat. At a broad scale, a parasite might attain higher densities in a forest than in more open habitats. At a narrow scale, such as within a forest, a parasite might be concentrated in a particular microenvironment such as a forest edge (Robb and Samuel 1990). Within a microenvironment, a parasite might aggregate preferentially on particular species of woody plant (Fourie et al. 1991). At the most narrow scale, an aggregation of a particular parasite, such as a species of tick, might be restricted to leaf surfaces or flower heads of the preferred woody plant (Chiera 1985, see review by Sousa and Grosholz 1991).

Because parasites have diverse life cycles, live in different habitat types, and use many and complex mechanisms to find hosts, the degree of influence by both abiotic and biotic factors on transmission to hosts varies among parasite species. Seasonal changes in structure and quality of habitat will alter the abiotic and biotic factors and thus affect the distribution, abundance and behavior of host and parasite and, consequently, the success of transmission.

Transmission of one major group of parasites, ticks, to hosts depends on the density, distribution and behavior of the host and the longevity and daily and seasonal activity patterns of the ticks (Sutherst et al. 1978). These factors are, in turn, influenced by habitat structure and meteorological conditions.

Ticks find their hosts either by 'ambushing'; *i.e.*, lie in wait at a strategic location for the hosts to pass, or by 'hunting'; *i.e.*, actively search for the hosts (Barnard 1991, de Castro 1991). Ticks that ambush hosts climb vegetation, position themselves near or at tips of leaves, stems, etc, and remain there until some external stimuli from a passing host elicit a questing behavior (Camin and Drenner 1978). Through questing (*i.e.*, waving of outstretched anterior legs in the direction of emitted host stimuli) ticks make contact with, and attach to, hosts. Host-seeking 'hunter' ticks move in the direction of the host after detecting host external stimuli. Because most hard ticks (*i.e.*, ticks in the family Ixodidae) have limited migratory ability, the ambush type of host-seeking predominates. Hence host activity and movement then become important factors in the host-tick contact process (Barnard 1991).

Patterns of host movement and habitat use were key factors in the transmission of Amblyomma hebraeum to a host (Rechav 1978), Dermacentor variabilis to deer mice, Peromyscus leucopus (Sonenshine and Stout 1968), Ixodes ricinus to sheep, Ovis sp. (Randolph and Steele 1985) and Amblyomma americanum to cattle, Bos spp. (Barnard 1989a). Also, weather factors have been reported to play important roles in the host-tick contact process and the transmission of many ixodid ticks such as Boophilus microplus (Sutherst et al. 1978), Haemaphysalis leporispalustris (Camin and Drenner 1978), A. americanum (Barnard 1989a, b), Ixodes pacificus (Loye and Lane 1988, Lane and Stubbs 1990) and Dermacentor occidentalis (Lane et al. 1985).

An important tick for which little information on transmission is available, is the winter tick, Dermacentor albipictus. Common hosts include white-tailed deer (Odocoileus virginianus), mule deer (O. hemionus), elk (Cervus elaphus) and moose (Alces alces) (Welch et al. 1991). However, it is on moose that winter tick is a serious pest, causing damage to winter hair coat (McLaughlin and Addison 1986, Samuel et al. 1986, Samuel 1991), anemia and other physiological effects (Glines and Samuel 1989), reduced fat stores (McLaughlin and Addison 1986), and morbidity and mortality (Samuel and Barker 1979, Samuel et al. 1986, Blyth and Hudson 1987, Glines and Samuel 1989). Epizootics of winter tick infestations on moose in Elk Island National Park (EINP) and other parts of Alberta have resulted in significant mortality of moose (Samuel and Barker 1979, Blyth and Hudson 1987, Samuel, pers. commun. 1994). There are five ungulate species in EINP; bison (Bison bison), elk, moose, white-tailed deer and mule deer, but moose is the principal host of winter tick (Welch et al. 1991). Any management plan for moose where winter tick is enzootic should include the control of the tick. However, "ecological understanding of the nature of the problem" is fundamental to designing control strategies (Sutherst 1989).

Winter tick is a one-host tick; *i.e.*, all parasitic life stages occur on the same individual. In Alberta, on moose, adult female ticks that have fed on blood drop off during early spring and lay eggs in late spring (Gline and Samuel 1984, Drew and Samuel 1986, 1989). Eggs hatch to larvae in late summer (Drew and Samuel 1986). After a short diapause (during which time larvae apparently remain in the leaf litter), larvae ascend vegetation and form aggregations (Wilkinson et al. 1982, Drew and Samuel 1985).

Transmission from vegetation to moose occurs between September and November (Drew and Samuel 1985). The larvae, once on moose, quickly feed and molt into nymphs (Drew and Samuel, 1989). Nymphs molt into adults during winter. Adults engorge on blood thus completing the cycle (Glines and Samuel 1984, Addison and McLaughlin 1988, Drew and Samuel 1989) (Figure 1.1).

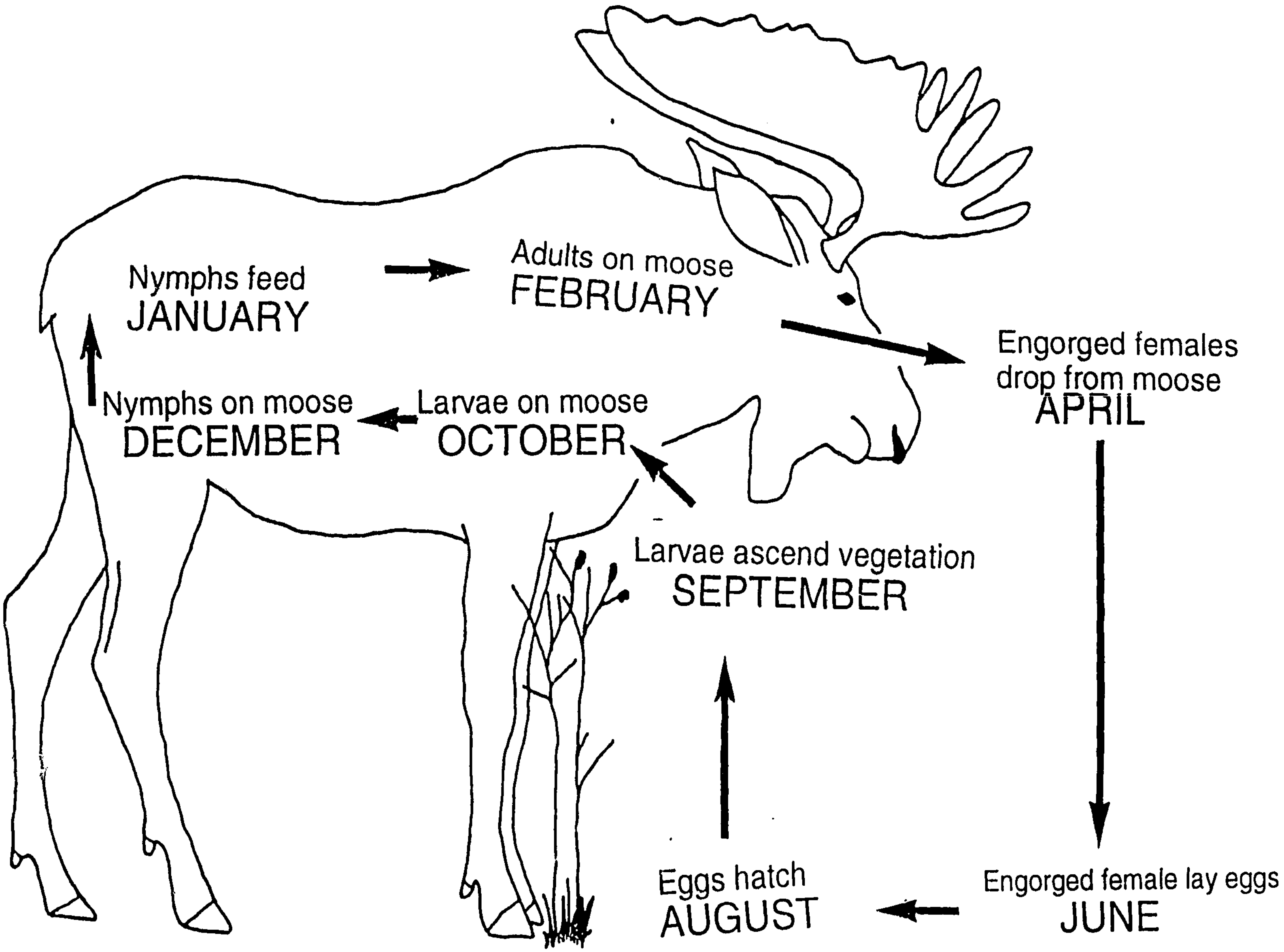
Distribution and habitat selection of moose during the different seasons in various regions of North America have been documented in detail (Krefting 1974, Joyal 1987, Ballard et al. 1991, Renecker and Hudson 1992), but the influence of movement and habitat selection by moose on transmission of winter ticks in EINP is unknown. Movement and habitat selection by moose during early spring and early autumn when engorged female ticks are dropping from moose and tick larvae are on vegetation, respectively are critical in the transmission dynamics of winter tick in EINP.

OBJECTIVES

This study was designed to determine the influence of abiotic and biotic factors on the host-tick contact process and transmission of D. albipictus to moose in EINP. It deals primarily with aspects of non-parasitic replete female ticks that have dropped from moose and larvae on vegetation seeking contact with and attachment to moose. The study addresses the following objectives:

1. To determine the distribution, abundance and density of winter tick larvae in the major habitat types in Elk Island National Park;
2. To determine the longevity of winter tick larvae in those habitat types;

Figure 1.1 Life cycle of D. albipictus in central Alberta (Months represent peak period of cycle event) (Modified from Drew and Samuel 1989)


Nymphs feed
JANUARY
Adults on moose
FEBRUARY
Engorged females
drop from moose
APRIL
Engorged female lay eggs
JUNE
Eggs hatch
AUGUST
Larvae ascend vegetation
SEPTEMBER
Larvae on moose
OCTOBER
Nymphs on moose
DECEMBER

3. To assess the influence of moose distribution and habitat selection on distribution and abundance of tick larvae;
4. To determine the questing activity of larval winter ticks under field conditions,.
5. To assess the influence of habitat types on the survival and reproduction of replete female winter ticks in the Park.

The following hypotheses were tested:

H1. Larvae of D. albipictus are evenly distributed and equally abundant in the different habitat types of EINP.

H1a. Larvae of D. albipictus are not evenly distributed and equally abundant in the different habitat types of EINP.

Prediction: Larvae of D. albipictus will be more abundant in some habitat types than others because 1) selection of habitat by moose during late winter-early spring when adult female ticks are dropping from moose will be diferrent among habitat types and 2) microclimatic conditions that affect the survival and reproduction of engorged female ticks should also differ in the various habitat types.

H2. Longevity of D. albipictus larvae is the same in the different habitat types.

H2a. Longevity of D. albipictus is different in the different habitat types.

Prediction: Because longevity of tick larvae depends on weather, and microclimatic conditions differ by habitat type, longevity of larvae should differ by habitat.

H3. Moose distribution, density and habitat selection have no effect on D. albipictus larvae distribution, abundance and density in the habitat types.

H3a. Moose distribution, density and habitat selection have direct effect on D. albipictus larvae distribution, abundance and density in the different habitat types.

Prediction: Moose distribution and movement in early spring are localized and limited, and moose spend more time in selected habitats either feeding or resting. More engorged female tick D. albipictus will drop in such habitats. Also more engorged female ticks will drop in habitats and sites of high moose density than low moose density habitats and sites. Therefore, larvae will be more prevalent and abundant in habitats used by moose in spring than in habitats used by moose in autumn. Therefore moose distribution, density and habitat selection will have direct effect on larval distribution, abundance and density in the habitat types.

H4 There is no difference in the survival and reproductive characteristics of replete female winter ticks among the different habitat types of EINP.

H4a Survival and reproductive characteristics of replete female winter tick differ among the different habitat types.

Prediction: Microclimate of a habitat type influences the survival and reproduction of ticks. Different microclimatic conditions exist in the different habitat types. Habitat types with optimum temperature (> 15.1 C < 30.0 C) and moisture (80%) conditions, such as wooded habitats, will provide higher survival and higher reproduction potential for replete female ticks.

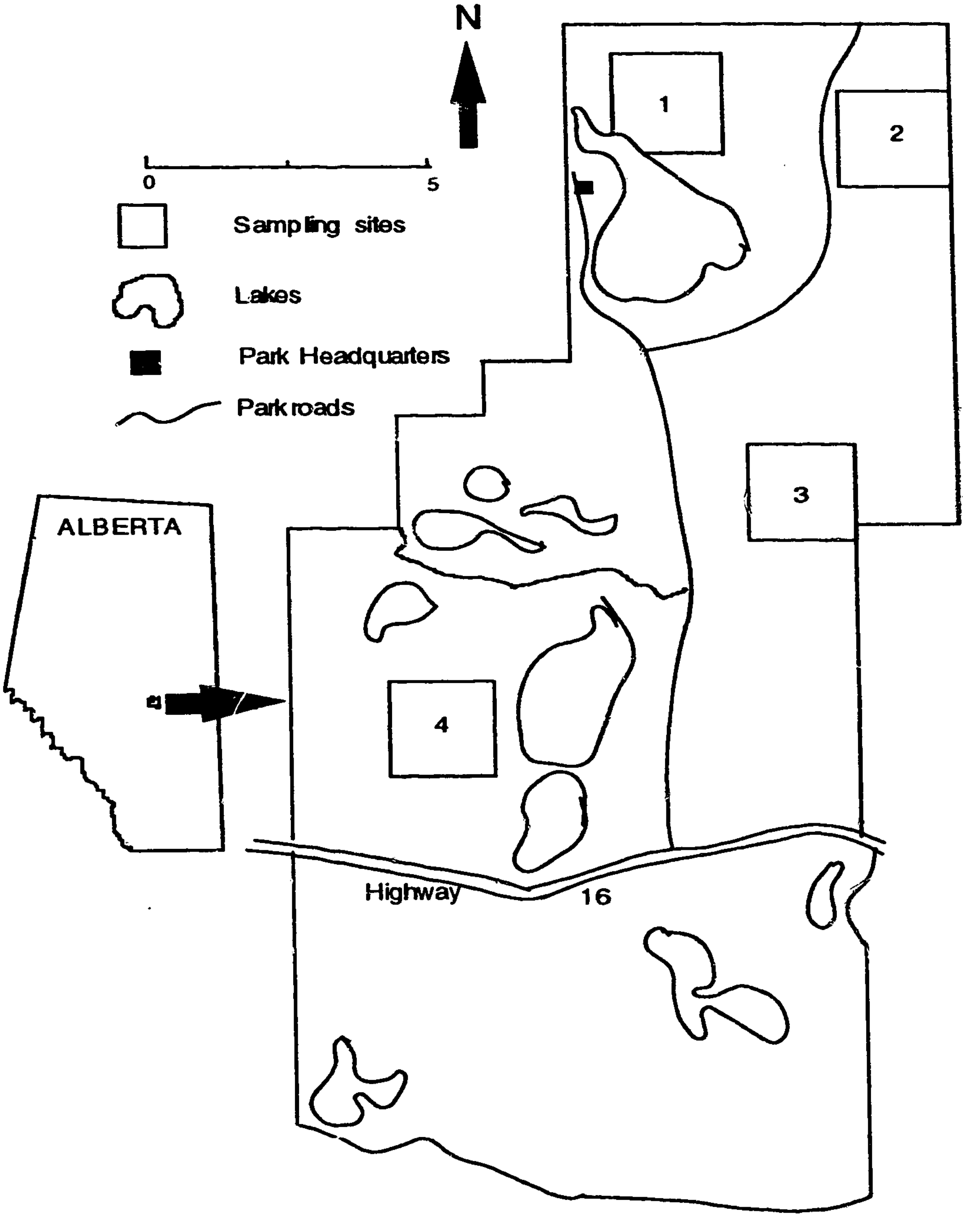
STUDY AREA

Elk Island National Park is located about 45 km east of Edmonton, Alberta. The park is divided by Highway 16 into a northern Main Park (132 km^2) and a southern Isolation Area (59 km^2) (Figure 1.2). Both sections are fenced with a 2.2 m high paige wire perimeter fence.

Weather conditions in EINP are similar to that of Edmonton though slight daily, monthly and yearly variations exist. Mean winter temperature ranges between -17.3 and -16.5 °C. Mean temperature in spring and autumn is about 0 °C. Frost-free days average about 120 days. Average temperatures in summer range between 10.6°C and 16.4°C (Blyth and Hudson 1987). Weather records collected in 1982 and 1983 indicate that temperatures vary among habitat types in EINP (Drew 1984). A bog habitat experienced longer periods of temperature above 15 °C compared to an aspen forest habitat and grassland habitat. Daily temperature variation was lowest in aspen forest because canopy cover prevents direct incidence of solar radiation while 'open' habitats such as bog and grassland, receiving direct solar radiation showed great variability in daily temperature (Drew 1984).

Annual precipitation around Edmonton, including EINP, is about 529 mm of which about 75% is rain, that falls between April and October; the rest is snow that falls

Figure 1.2 Location of Elk Island National Park in central Alberta with locations of sites where D. albipictus larvae were collected, 1991 - 1992.


N
0
5
Sampling sites
Lakes
Park Headquarters
Park roads
1
2
3
4
ALBERTA
Highway 16

between October and April (peak snowfall is between December and February) (Blyth andHudson 1987). Like other parts of Edmonton, strong winds (> 20 kph) generally blow from northwest while frequent but mild winds blow from the south (Olson 1985).

Geomorphologically, the Park is situated on the northern portion of the Cooking Lake Moraine about 30-50 m higher than the surrounding Alberta plains (Blyth and Hudson 1987). General landscape of the Park, as shaped by geological history, is a complex mosaic of small hummocks, prairie mounds, linear ridges with some interspersed flat lying glaciolacustrine areas. The soils of the Park are described generally as chernozemic and solonetzic but local parent rock material and vegetation have influenced the formation of Gray Luvisolic soils (Blyth and Hudson 1987).

The presence of a perimeter fence has restricted movement and dispersal of the five ungulate species out of the Park. The high densities of these animals make EINP one of the overstocked parks in North America (Blyth, unpubl. data). Intensive management of animal populations was therefore initiated in 1928 and continued through the 1980's; it included harvests and translocations to restock other areas. These management practices have kept the animal populations within the carrying capacity of the Park (Blyth unpubl. data). Now only live trapping of animals and vegetation management through prescribed burning are used to manipulate animal.

The vegetation of EINP is dominated by aspen (Populus tremuloides, P. balsamifera), birch (Betula papyrifera). There are pockets of spruce (Picea mariana). Common shrubs in the park include hazelnut (Corylus cornuta), prickly rose (Rosa acicularis), willow (Salis spp.). Sedges (Carex spp.) are also common. A few grasses such as reed grasses (Calamagrostis spp.), blue grasses (Poa spp.) occur infrequently (see review by Blyth and Hudson 1987). The classification of the vegetation of EINP is complex as seen from the different opinions expressed by many authors (reviewed by Blyth and Hudson 1987). This suggests that the composition and structure of vegetation have gone through considerable succession since the Park was established in 1906. Approaches to classification have also varied according to the purpose of a study (Cairns 1976, Drew 1984, Reid 1986, Blyth and Hudson 1987). A vegetation classification that reflects different microclimatic conditions among "class" types is most adequate for this study. A recent study (Reid 1986) classified vegetation of EINP as 'Parkland - Boreal Forest Transition Zone'. This and other studies (Trottier and Nagy 1974, Polster and Watson 1979) recognised and described the physiognomy of the vegetation and mapped the vegetation into different habitat types.

For this study, the habitat types described by Cairns (1976), Reid (1986) and Blyth and Hudson (1987) were recategorized into eight habitat types that differ physiognomically among one another and consequently reflect differences in microclimatic conditions. The eight are: closed aspen forest (AC), open aspen forest (AO), grassland (GR), labrador tea (LT), spruce forest (black and white spruce) (SF), shrubland (SH), sedge bog (SB) and willow bog (WB). These habitats are described below.

Closed aspen forest (AC)

This habitat type (Figure 1.3) constitutes about 30% of the park area. Tree layer is mainly aspen poplar (P. tremuloides) and balsam poplar (P. balsamifera) with diameter greater than 5.0 cm at breast height (dbh). Tree density ranges from 769-917 per hectare with canopy closure between 40 - 100% (Blyth and Hudson 1987). The understorey cover consists mainly of shrubs such as hazelnut (C. cornuta) and wild rose (Rosa spp.) the density and height of which depend on the canopy closure of the existing aspen forest. Shrubs may be absent in some areas and their place taken by reed grasses (Calamagrostis spp.).

Open aspen forest (AO)

This habitat (Figure 1.4) occupies abou˙ 34% of the park area. Tree layer consists of aspen poplar (P. tremuloides), and poplar balsam (P. balsamifera) as in closed aspen but canopy closure is between 10 - 40%, tree density is about 115 per hectare and dbh larger than closed aspen (Blyth and Hudson 1987). Understorey cover comprises of many shrub species such as hazel (C. cornuta), willow (Salis spp.), saskatoon (Amelanchier alnifolia), cranberry (Viburnum edule), rose (Rosa acicularis), goosebery (Ribes spp.), raspberry (Rubus spp.), honeysuckle (Lonicera spp.), buckbrush (Symphoricarpos albus) and saplings of aspen poplar and poplar balsam. Total shrub density is relatively high (18 per square meter). The proportion of shrubs varies with site conditions and the height of shrubs also depends on animal use, but generally, shrubs are about 1 m tall (Blyth and Hudson 1987).

Figure 1.3 Closed aspen forest habitat in Elk Island National Park, Alberta.

Figure 1.4 Open aspen forest habitat in Elk Island National Park, Alberta.

Grassland (GR)

This habitat type (Figure 1.5) occupies about 9% of the park area. Grasslands are distributed as small openings in the forests or along south facing slopes. Species composition varies at different sites and consists of both agricultural and native varieties (Blyth and Hudson 1987). Common agricultural grass varieties include: timothy (*Phleum pratense*), wild barley (*Hordeum jubatum*), quack grass (*Agropyron repens*), brome (*Bromus* spp.) and blue grass (*Poa* spp.). Leguminous species include clovers (*Trifolia* spp.) and medick (*Medicago* spp.). Common native species include: wheat grass (*Agropyron* spp.) and reed grass (*Calamagrostis* spp.) (Blyth and Hudson 1987). Short grass species such as blue grass rarely measure to 1 m above ground and are usually patchy and interspersed among the taller grasses such as brome and reed grass.

Labrador tea (LT)

Labrador tea habitat (Figure 1.6) is very patchy in distribution and forms about 1% of the park area. Main vegetation is labrador tea (*Ledum* spp.), with scattered black spruce (*P. mariana*) or willow (*Salix* spp.). It is a lowland habitat usually associated with or bordered by black spruce (*P. glauca*) (Blyth and Hudson 1987). Because of high accumulation of peat, it is rarely waterlogged.

Spruce forest (SF)

This habitat type (Figure 1.7) represents small, isolated stands of both white spruce (*P. glauca*) and black spruce (*P. maraina*) which together make up about 2% of the park

Figure 1.5 Grassland habitat in Elk Island National Park, Alberta.

Figure 1.6 Labrador tea habitat in Elk Island National Park, Alberta.

area. The spruce forest habitat type consists of white spruce, black spruce, labrador tea (L. groenlandicum), swamp birch (Betula pumila), and tamarack (Latrix laricina). Canopy cover is 100% although open upland forest occasionally occur. Understory vegetation in open upland forest type includes few shrubs, grasses and herbs. Moss and lichen vegetation are typical undergrowth of a closed spruce forest otherwise, the forest floor is bare.

Shrubland (SH)

This habitat type (Figure 1.8) is dominated by shrubs and makes up about 4 % of EINP. Proportion of beaked hazelnut (C. cornuta) is higher (50%) than other shrubs such as rose and cranberry (Olson and Blyth 1985 in Blyth and Hudson 1987). Shrubs in this habitat type are usually taller than similar shrubs under either closed or open aspen forests, but the height is subject to the grazing pressure by ungulates. Grass species such as quack grass, blue grass, brome, and reed grass do occur at some sites but their density are inversely proportional to shrub density.

Sedge bog (SB)

This habitat type (Figure 1.9) comprises about 13% of EINP and occurs in flat lowland, usually water-logged, that is often bordered by willow shrubland. Main vegetation composition includes sedges such as awned sedge (C. atherodes), beaked sedge (C. rostrata) and grasses such as reed grass, manna grass (Glyceria spp.) and blue grass whose proportions depend on the locality. Height of both sedge and grass also depend on the locality. Patches of willow of various stature are occasionally present and this also depends on locality.

Willow bog (WB)

This habitat (Figure 1.10) comprises about 4% of EINP and is dominated by mainly willow shrubs and occur in low and wet locations. Height of willow is about 3 m tall. Low stature willow sites are also common. Understory vegetation consists of sedge and grass in varying proportions which may be quite sparse depending on the canopy cover of willow. Canopy of willow cover can reach 100% in some locales. This habitat type most times forms an interface between a sedge bog and aspen forest.

Figure 1.7 Spruce forest habitat in Elk Island National Park, Alberta.

Figure 1.8 Shrubland habitat in Elk Island National Park, Alberta.

Figure 1.9 Sedge bog habitat in Elk Island National Park, Alberta.

Figure 1.10 Willow bog habitat in Elk Island National Park, Alberta.

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CHAPTER TWO

INFLUENCE OF HABITAT TYPE AND MOOSE DENSITY ON DISTRIBUTION AND ABUNDANCE OF WINTER TICK (*DERMACENTOR ALBIPICTUS*) (ACARI: IXODIDAE), LARVAE IN ELK ISLAND NATIONAL PARK, ALBERTA.

INTRODUCTION

Many recent studies of tick ecology deal with ticks of Africa (*e.g*, Sutherst 1987, Dipeolu 1989, Pegram et al. 1989, Fourie et al. 1991, Randolph 1993), Boophilus microplus of Australia (*e.g.*, Sutherst and Maywald 1985, Sutherst et al. 1986, 1988a, b, Sutherst 1989), Amblyomma americanum in the southern United States (*e.g.*, Haile and Mount 1987, Barnard 1991, Mount et al. 1993) and Ixodes scapularis (= I. dammini), the vector of Lyme disease, in central North America (*e.g.*, Burgdorfer et al. 1988, Schulze et al. 1988, Siegel et al. 1991). There are few recent studies of tick ecology in Canada, particularly Western Canada, except for work on winter tick, Dermacentor albipictus (Samuel and Welch 1991 and papers cited therein) and Rocky Mountain wood tick, Dermacentor andersoni (Schaalje and Wilkinson 1985).

One important aspect of tick ecology is how habitat affects tick distribution and abundance (Semtner et al. 1971, Semtner and Hair 1973, Carey et al. 1981, Schulze et al. 1984, Ginsberg and Ewing 1989, Adler et al. 1992, Stafford and Magnarelli 1993). Habitat is important because it influences the distribution and abundance of vertebrate hosts, the microclimatic conditions of site that affect survival of free-living tick life stages and reproduction of female ticks, and provides vegetational microsites from which host-seeking ticks ambush passing vertebrate hosts (Barnard 1991, de Castro 1991). Abundance of ticks in a particular habitat is a reflection of the combined effects of biotic and abiotic components in that habitat (Semtner and Hair 1975, Barnard 1991, Adler et al. 1992). It depends on the distribution and density of vertebrate hosts, and survival of free-living tick life stages in those habitats (Barnard 1991, Randolph 1993). Again, there are few northern studies (Wilkinson 1967, Drew and Samuel 1986).

The winter tick, in Alberta, is near its northern distributional boundary (Samuel 1989). Nonetheless, it is very numerous on its primary host, the moose, *Alces alces* (Samuel and Welch 1991, Welch et al. 1991), and is often involved in major die-offs of moose (Samuel and Barker 1979, Blyth and Hudson 1987). Although Drew and Samuel (1986) state that "winter ticks must be very efficient in using available habitats and favorable environmental conditions to survive," there are few data on how habitat might affect population size of winter ticks. In this chapter I summarize results of a 2-year study on the distribution and abundance of winter tick larvae in eight habitat types in areas of high (three sites) and low (one site) moose densities in Elk Island National Park (EINP). Results are based largely on collection of tick larvae in autumns, 1991-1992, along line transects.

OBJECTIVES

The main objectives of the present study were to determine numbers of winter tick larvae in eight habitat types in EINP during the transmission season in autumn, when tick larvae are on vegetation and whether or not moose distribution and density during spring, when adult female ticks are dropping from moose, had any influence on the distribution and abundance of tick larvae. Specific objectives of the study were to:

1) assess the distribution, abundance and density of winter tick larvae in eight habitat types within four 4 km^2 sites of high moose density (three sites) and low moose density (one site),

2) evaluate the effects of weather (temperature, relative humidity, and wind) on the success of collecting winter tick larvae, and

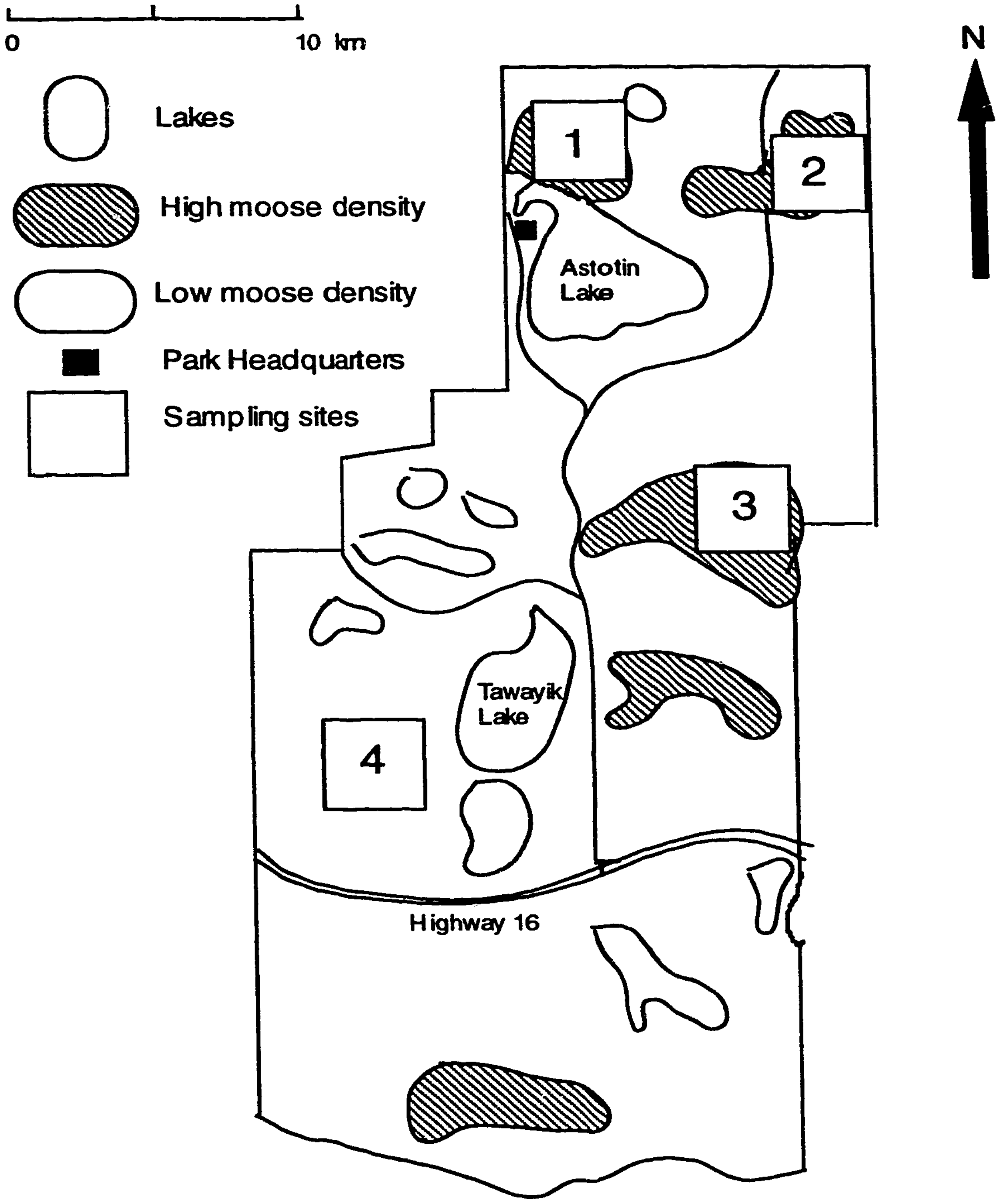
3) assess the abundance of winter tick larvae during 3 mo (September, October and November 1992) of the transmission season of winter tick in EINP.

METHODS

Sampling design

The study was conducted in the Main Park (*i.e.*, north of Highway 16) (Figure 1.2, p. 10). Four sites, each 4 km^2, were selected arbitrarily in areas of high (three sites) and low (one site) moose density. Selections were based on estimated number of moose in winter, 1990 - 1991 (Figure 2.1) (Unpublished report, EINP, 1991) and proximity to park trails, that provided reasonably good access to sites. Estimated densities of moose for Sites 1-3 and Site 4 were: 2-4/km^2 and $<$ 2/km^2, respectively. Chosen sites were located on topographical map (1:50,000). Compass bearings and distances from one corner of each site to a reference point on a park trail were calculated on the map. The distance from the nearest road to each reference point on trail was also determined. Sites were

Figure 2.1 Estimated densities of moose in Elk Island National Park during winter of 1990-1991 (Unpublished Park Report, 1991).


0
10 km
Lakes
High moose density
Low moose density
Park Headquarters
Sampling sites
N
1
2
Astotin Lake
3
Tawayik Lake
4
Highway 16

located on the ground by measuring the distance from a road to the reference point on a trail and then reading a calculated compass bearing and measuring the distance to the corner of the site. A 2 km baseline for each site was measured in either north-south or east-west direction depending on the site. Both ends of the baseline were identified with markers. The same sites were used for collection of larvae in autumn 1991 and 1992.

Site 1, north of Astotin lake, represented all habitat types but open aspen was dominant. It was a high moose density site. Site 2 was located between the park road (1km south of north gate) and the eastern Park boundary. Closed aspen dominated at this site which was also termed a high moose density site. Site 3 was selected along the eastern Park boundary. It was a high moose density site dominated by closed aspen. Site 4 was located west of Tawayik lake. It was a high elk density but low moose density site. Dominant vegetation was closed aspen. All four sites were equally rugged topographically with many bogs and lakes (see chapter 1).

Each site was divided into 2,000 transects, 2 km long and 1 m apart, perpendicular to the baseline. Four transects were selected at random from computer generated random numbers each day for each site. Each selected transect was divided into 80 25 m units and 10 units were selected randomly (also from computer generated random numbers) and flagged with flannel cloths to collect tick larvae. Flannels from each unit are hereafter called samples. Each site was sampled once a week from September 18 to November 6, 1991 and September 2 to December 10, 1992. True compass bearings were used to determine direction of baselines and transect lines. A hip-chain was used to measure distances of each transect and sample unit. Reference point at either end of the baseline for a day's sampling was always determined by toss of a coin.

Habitat types (see chapter 1) were recategorized from classifications by Polster and Watson (1974), Cairns (1976) and Reid (1986).

Attempting to walk 8 km of transects, and collect flannel samples from 40 25 m units on the transects, proved very demanding on energy and time. As a result I ran out of daylight on some days in both years and could not complete all transects. In addition, 2 d of sampling were missed at each site between October 16 - 26, 1991, due to very bad weather. In 1992, Sites 2 and 3 were not sampled on September 4 and 5, respectively, due to very bad weather. Site 3 was not sampled on October 31, 1992 because of a transportation problem. The result was that I collected 599 of the projected 960 samples in 1991 and 1556 of a projected 2240 samples in 1992.

Sampling technique

To collect tick larvae, I dragged a 1 m^2 white flannel cloth across vegetation that was less than 1.5 m high. The flannel, attached to a dowel, was carried at my side. Each 2 km transect line traversed several habitat types. Before flagging each sample unit, the time, temperature, relative humidity, wind intensity and habitat type of the unit were recorded. In 1991, temperature was measured, at about 1 m above ground, using a portable Maximum and Minimum Thermometer (psychometric-dial; model CP 147). Relative humidity was determined from the maximum and minimum temperature readings from a calibrated scale. Wind intensity was assessed as strong (>20 km), mild (10 - 20 km), or nil (<10 km). In 1992, temperature and relative humidity were measured, at 1m above ground, using a hand-held HM 34 Temperature and Humidity Indicator (Vaisala Instruments, Helsinki, Finland). Wind intensity was again assessed as strong, mild or nil.

A clean (tick-free) flannel was used to flag each sample unit. After flagging each unit, the flannel was examined for tick larvae. Flannels with larvae, hereafter called positive flannels, were folded and put into a labelled polythene bag.

In both years, distances of baselines, transects and sample units were measured using a hip-chain worn on the waist. A piece of biodegradable thread from the hip-chain was tied to a twig at the start of every measurement and the distance read from a meter on the hip-chain.

In 1991, positive flannels collected before October 15 were brought to the University of Alberta, stored in a freezer and larvae were counted after the field season. Positive flannels collected after October 15 (*i. e.*, the post-storm period) were taken to the university and the few tick larvae found were counted that day. In 1992, positive flannels were taken to the university and tick larvae found were counted that same day. In that way, survival of larvae, as well as numbers, could be determined. During the count, the flannel was spread on a white background under an illuminated magnifying glass (2X). Numbers of tick larvae were recorded on a manual counter and larvae were removed from the flannel with a lint roller.

DATA ANALYSIS

Data analysis was performed using SYSTAT 5.0 software (Wilkinson 1990) on a personal computer. Data were analyzed separately for each year unless stated otherwise.

The proportions of sample units among habitat types were compared among sites using X^2 test. Habitat types that occurred at low frequency were pooled to maintain expected frequencies ≥ 5 in all cells.

Three aspects of the occurrence of tick larvae were evaluated:

1) distribution,

2) abundance, and

3) density.

Distribution is the frequency of occurrence of positive flannels in an area (= habitat or site); *i.e.*, the number of positive flannels divided by the total number of flannels examined. Distribution data are expressed as percent and are intended to assess the probability of encountering clumps of tick larvae within habitat types and sites.

Abundance is relative density; *i.e.*, the mean number of tick larvae per flannel examined in an area (habitat or site). It is intended as an index to the number of tick larvae that might be acquired by hosts moving within or among habitat types and sites during the transmission season.

Density is the mean number of larvae on positive flannels from an area (habitat or site). It is intended to assess the number of tick larvae that might be acquired if a clump of larvae was encountered by a host.

Distribution of winter tick larvae among habitat types and among sites was evaluated by comparing number of positive to negative flannels using a G test. Low frequency categories were pooled to maintain expected frequencies ≥ 5. In cases where heterogeneity was detected, X^2 tests on individual cells were conducted (df = 1) to identify categories that differed.

Abundance data were not distributed normally because of the inclusion of large numbers of negative flannels. These values could not be transformed to meet the assumption of ANOVA, so were analyzed using non-parametric equivalents, the Kruskal-Wallis and Mann-Whitney tests. Abundance of winter tick larvae was compared among habitat types and among sites for 1991 and 1992 and in 1992, among three time categories (September, October, November) using Kruskal-Wallis one-way anova test. Not enough data were collected to make the same comparison in 1991. When a Kruskal-Wallis test revealed a significant difference among three or more groups, pairwise Mann-Whitney U-tests were performed to detect groups that differed. The Bonferroni procedure was used to maintain the experimentwise error rate of $a = 0.05$ when performing these multiple comparisons. Where a group was compared to $\underline{n}$ other groups, the results for an individual test were accepted as significant only if $P < a/\underline{n}$ for the individual test.

Density of tick larvae was evaluated and compared among habitat types in only 1992 (insufficient data in 1991) using ANOVA on log-transformed data. Data for October were used because this was the peak of larval tick abundance. In September not all larval ticks had ascended vegetation and in November most tick larvae had acquired host or died. The assumption of homogeneity of variances was tested on log-transformed data by Bartlett's test. Where an overall ANOVA indicated significant differences in density, multiple pairwise comparisons were done using Tukey's HSD test. The hypothesis of no significant difference was rejected at $P \leq 0.05$.

Density of tick larvae in the habitat types during the period September 18 to October 14, 1991, was compared with similar period in 1992 using t-test. Again, this time period was chosen because a major snowstorm in mid-October, 1991, essentially ended recovery of tick larvae.

Relationship between number of tick larvae collected by flagging and temperature, relative humidity and wind was tested by Stepwise forward multiple regression analysis. The duration tick larvae survived in each habitat type was estimated as the number of days between the day the first larva was collected and the day the last larva was collected in the habitat. The day the first dead larva was collected in each habitat was recorded.

RESULTS

Sampling intensity

A total of 599 and 1556 samples were collected from 25 m units in the four 4 km^2 sites in 1991 and 1992, respectively (Table 2.1). This sampling resulted in collection of about 17,000 and about 44,800 tick larvae in 1991 and 1992, respectively (Table 2.2). Although there were differences in 1991 and 1992 in the number of samples among the eight habitat types in the four sites ($X^2 = 73.97$, df = 18, $P < 0.001$ for 1991 and $X^2 = 136.00$, df = 18, $P < 0.001$ for 1992), the overall ratio of sampling was similar between years (Table 2.1, Table 2.3, and Figure 2.2). Only labrador tea and spruce forest habitats were not encountered at all four sites during both years (Figure 2.2). The two aspen habitats, closed and open, were sampled in greater number in 1991 and 1992 than other

Table 2.1 Number of flannel sample units collected during sampling for D. albipictus larvae along transects at four sites in Elk Island National Park, 1991 and 1992.

	1991	1992
Sites	Number (% of total)	Number (% of total)
1	132 (22.0)	422 (27.1)
2	157 (26.2)	389 (25.0)
3	146 (24.4)	308 (19.8)
4	164 (27.4)	437 (28.1)
	599 (100)	1556 (100)

Table 2.2 Total number of *D. albipictus* larvae collected by flagging at three high moose density and one low moose density sites during tick transmission season, Elk Island National Park, Alberta, 1991 and 1992.

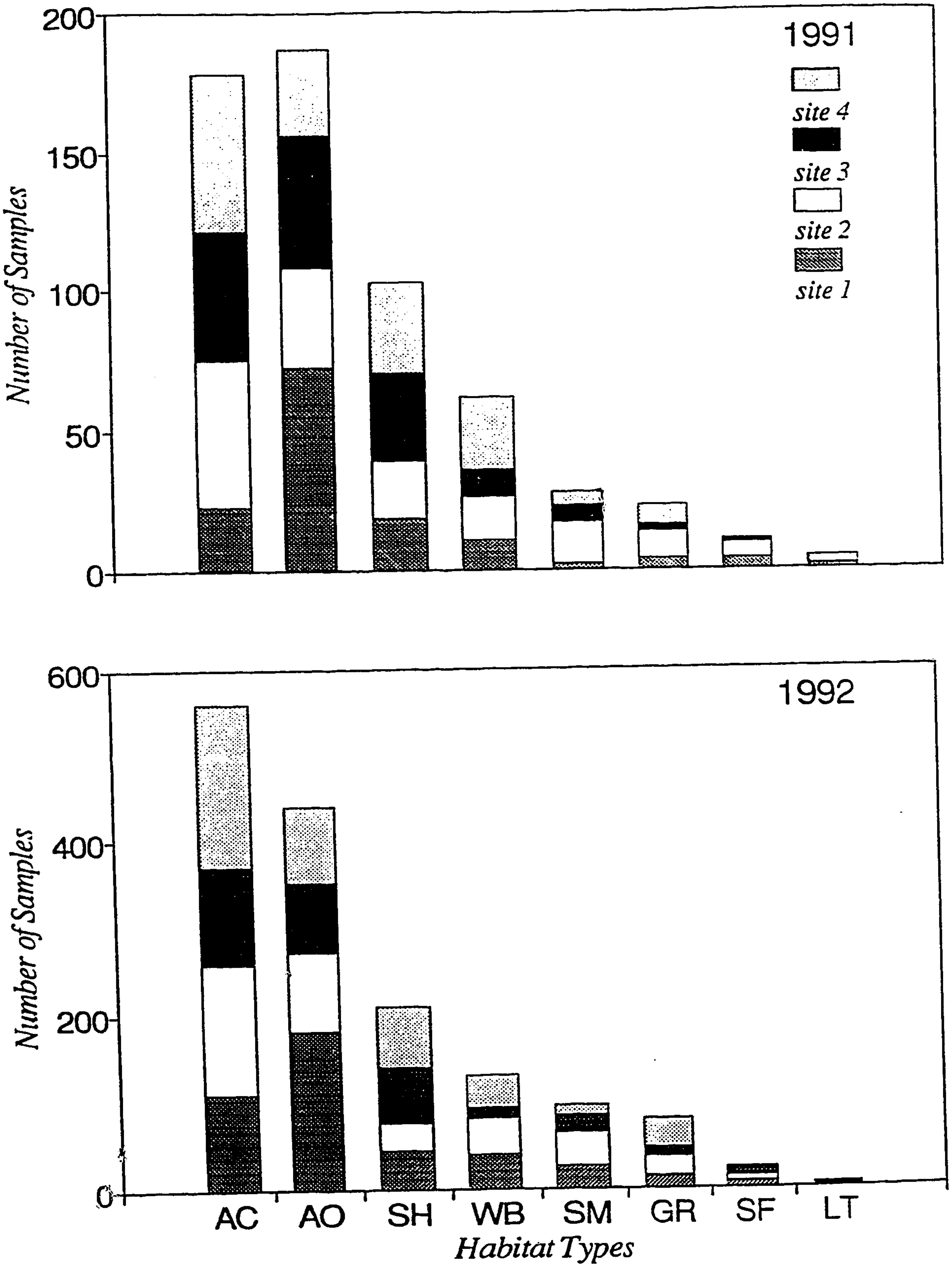
	Sites									
	1		2		3		4		Total	
Date	1991	1992	1991	1992	1991	1992	1991	1992	1991	1992
Sept.1 - 15	-[1]	347	-	68	-	160	-	262	-	837
16 - 30	1373	1815	3929	984	4415	2848	1738	1746	7481	7393
Oct. 1 - 15	1561	8983	2176	2766	1089	2982	1131	4019	5957	18750
16 - 31	1	3927	-	1118	-	3007	19	3066	20	11118
Nov. 1 - 15	0	2559	0	766	0	989	0	587	0	4901
16 -30	-	1359	-	305	-	105	-	24	-	1793
Dec. 1 - 10	-	2	-	21	-	5	-	8	-	36
Total	6535	18992	6105	6028	4416	10096	2888	9712	17058	44828

[1] No data were collected within the period.

Table 2.3 Number of flannel sample units collected during sampling for D. albipictus larvae along transects in eight habitat types at four sites of Elk Island Park Alberta, 1991 and 1992.

Habitat types	1991 Number (% of total)	1992 Number (% of total)
Closed aspen	178 (29.7)	560 (36.0)
Open aspen	188 (31.4)	442 (28.4)
Grassland	23 (3.8)	80 (5.1)
Labrador tea	5 (0.8)	7 (0.4)
Spruce forest	11 (1.8)	25 (1.6)
Shrubland	103 (17.2)	211 (13.6)
Sedge bog	29 (4.8)	99 (6.4)
Willow bog	62 (10.4)	132 (8.5)
	599 (100)	1556 (100)

Figure 2.2 Sampling effort for collecting D. albipictus larvae in eight habitat types at four sites in Elk Island National Park, 1991 - 1992 (AC = closed aspen forest, AO = open aspen forest, SH = shrubland, WB = willow bog, SB = sedge bog, GR = grassland, SF = spruce forest, LT = labrador tea).


200
150
100
50
0
Number of Samples
1991
site 4
site 3
site 2
site 1
600
400
200
0
Number of Samples
1992
AC
AO
SH
WB
SM
GR
SF
LT
Habitat Types

habitats. Labrador tea was the least sampled habitat in both years (Table 2.3).

Many sample units were collected in a day at sites 2 and 4 which were nearer to park trails because of quick access and thus longer sampling period than at sites 1 and 3 which were far from park trails. Also long distances between transects, rough terrain and thick vegetation reduced the number of sample units collected at a site in a day.

Expectation of encountering certain habitats, based on their proportions in the Park, in certain sites was not always fulfilled. For example, in 1991, significantly fewer samples than expected were collected in closed aspen at Site 1 and open aspen at Site 4. Significantly more samples than expected were collected in open aspen at Site 1, sedge meadow at Site 2, and willow bog at site 4 (Figure 2.2). In 1992, significantly fewer samples than expected were collected in closed aspen in Site 1, open aspen at Site 2, sedge bog at Site 4, and willow bog at Site 3, while significantly more samples than expected were collected in closed aspen at Site 4, open aspen at Site 1, and grassland at Site 4. In 1992, fewer samples were collected from Site 3 than from other sites because 2 d of sampling (September 5 and October 31) were missed. In general, the proportions of habitat types sampled during 1991 and 1992 (Table 2.3) reflected the proportion of the habitat types in the Park according to Cairns (1976), Reid (1986), Blyth and Hudson (1987), and Cool (1992, unpubl. report and see chapter 1).

Distribution, abundance and density of winter tick larvae

Distribution and abundance of D. albipictus larvae did not differ among sites in 1991 ($G = 2.47$, $df = 3$, $P = 0.480$; $H = 2.16$, $df = 3$, $P = 0.540$, respectively), but were different in 1992 (G = 23.07, df = 3, P < 0.001; H = 30.02, df = 3, P < 0.001, respectively) (Table 2.4). Though abundance of tick larvae was different among sites in 1992, there was no consistent pattern based on moose density. In 1992, the distribution and abundance of tick larvae were significantly higher at Site 1 than the other sites (P < 0.017). No significant difference in either distribution or abundance was detected between pairs of other sites (P > 0.017). Neither site nor interaction between site and habitat had an effect on larval density in 1992 (F = 0.47, df = 3, P = 0.703; F = 1.17, df = 3, P = 0.301 respectively).

Distribution, but not abundance, of tick larvae differed among habitats[1] in 1991 (G = 9.95, df = 3, P = 0.019; H = 11.34, df = 3, P = 0.124 respectively) but they both differed among habitats[1] in 1992 (G = 30.86, df = 4, P < 0.001; H = 61.86, df = 4, P < 0.001, respectively) (Figure 2.3 and 2.4, Table 2.5). In 1992, differences in larval tick distribution were observed among habitat types at sites of high moose density (Sites 1, 2, and 3) (G = 11.57, df = 4, P = 0.021; G = 21.48, df = 4, P < 0.001; G = 21.10, df = 4, P < 0.001, respectively). Only distribution of tick larvae in closed aspen, shrubland and the pooled habitats differed among sites (G = 16.60, df = 3, P = 0.001: G = 11.71, df = 3, P = 0.008: and G = 16.72, df = 3, P < 0.001, respectively). Abundance of tick larvae was significantly greater in closed aspen than in grassland and pooled habitats (X^2 = 7.47, P < 0.008; X^2 = 20.16, P < 0.008, respectively) and in shrubland than in open aspen and grassland (X^2 = 7.83, P < 0.008; X^2 = 14.07, P < 0.008 respectively). Open

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[1] Data for grassland, labrador tea, spruce forest, sedge bog and willow bog habitats in 1991 were pooled because of the relatively low sample sizes in those habitats. The same was true in 1992 for labrador tea, spruce forest, sedge bog and willow bog.

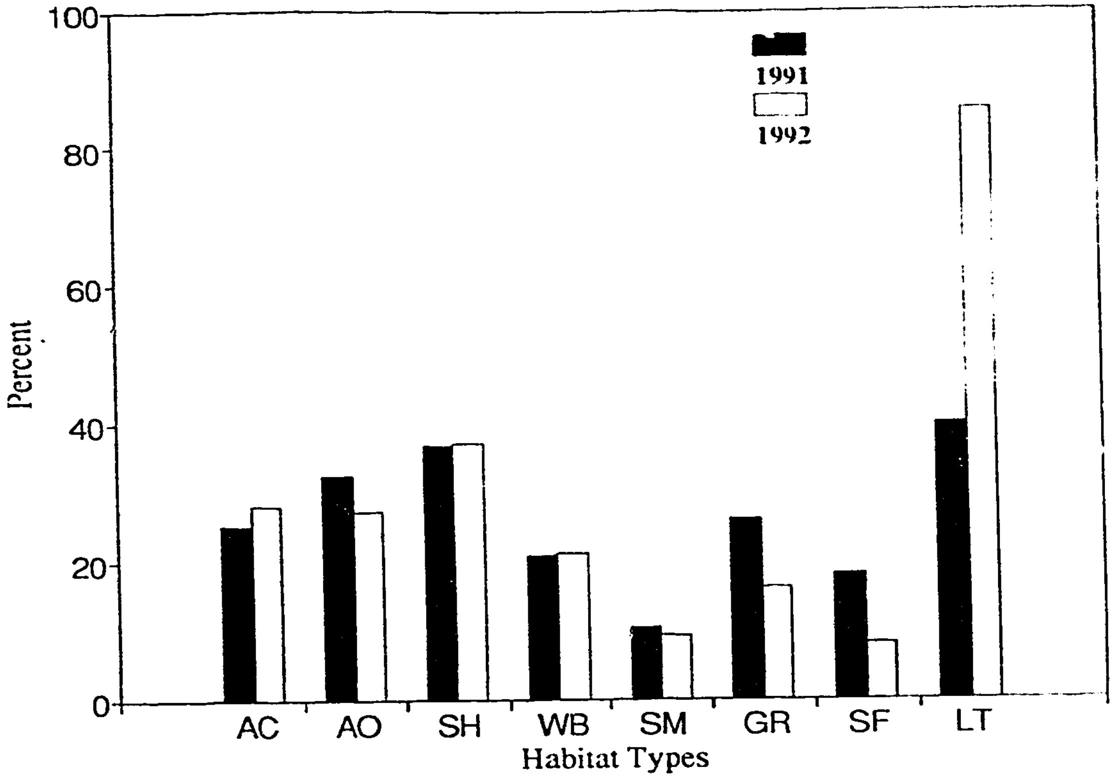
Table 2.4. Distribution, abundance and density of *D. albipictus* larvae in three high moose density and one low moose density sites of Elk Island National Park, Alberta, 1991 and 1992.

SITES	Distribution[1]		Abundance[2]		Density[3]	
	1991	1992	1991	1992	1991	1992
High moose density						
Site 1	30.3	35.8	57.0	43.9	188.1	122.8
Site 2	25.5	23.1	38.9	15.0	152.6	64.8
Site 3	23.3	27.6	37.7	32.0	161.9	116.1
Low moose density						
Site 4	30.5	22.7	17.6	21.8	57.7	96.0

[1] Percent positive flannel samples.
[2] Number of larvae/total flannel samples examined.
[3] Number of larvae/positive flannel samples examined.

Figure 2.3 Prevalence (expressed as percent) of D. albipictus larvae in eight habitat types in Elk Island National Park, 1991 and 1992.

Figure 2.4 Mean number (abundance) of D. albipictus larvae collected in eight habitat types in Elk Island National Park, 1991 and 1992.


1991
1992
100
80
60
40
20
0
Percent
AC
AO
SH
WB
SM
GR
SF
LT
Habitat Types

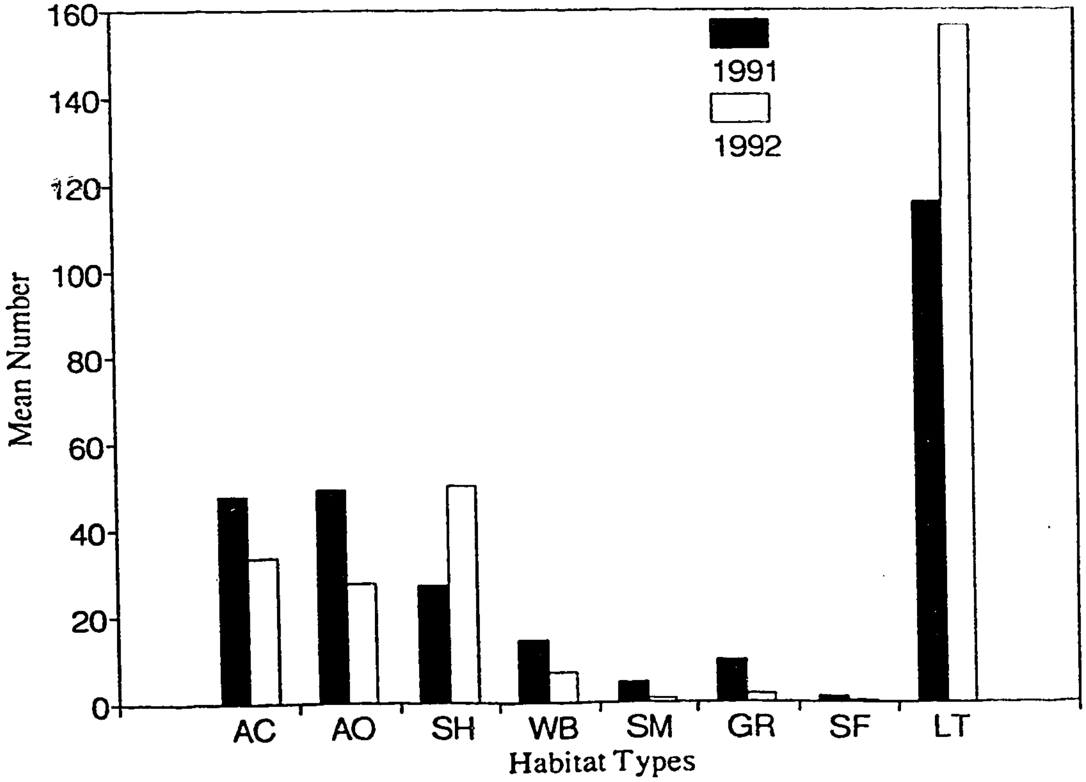

1991
1992
160
140
120
100
80
60
40
20
0
Mean Number
AC
AO
SH
WB
SM
GR
SF
LT
Habitat Types

Table 2.5 Distribution, abundance and density of D. albipictus larvae in eight habitat types at four sites in Elk Island National Park, Alberta, 1991 and 1992.

	Distribution[1]		Abundance[1]		Density[1]	
Habitat type	1991	1992	1991	1992	1991	1992
Closed aspen	25.3	28.0	48.0	33.6	190.0	119.7
Open aspen	32.4	27.2	49.1	27.4	151.2	100.9
Grassland	26.1	16.3	9.6	1.9	36.7	11.8
Labrador tea	40.0	85.7	115.6	156.3	289.0	182.3
Spruce forest	18.2	8.0	1.5	0.1	8.5	1.0
Shrubland	36.9	37.0	26.6	50.4	72.0	136.4
Sedge bog	10.3	9.2	4.7	0.7	45.0	7.2
Willow bog	21.0	21.2	14.3	6.8	68.4	32.1

[1] Data for grassland, labrador tea, spruce forest, sedge bog and willow bog were pooled in 1991 and data for labrador tea, spruce forest, sedge bog and willow bog were pooled in 1992 for statistical analyses.

aspen also had more tick larvae than pooled habitats (X^2 = 16.35, P < 0.008).

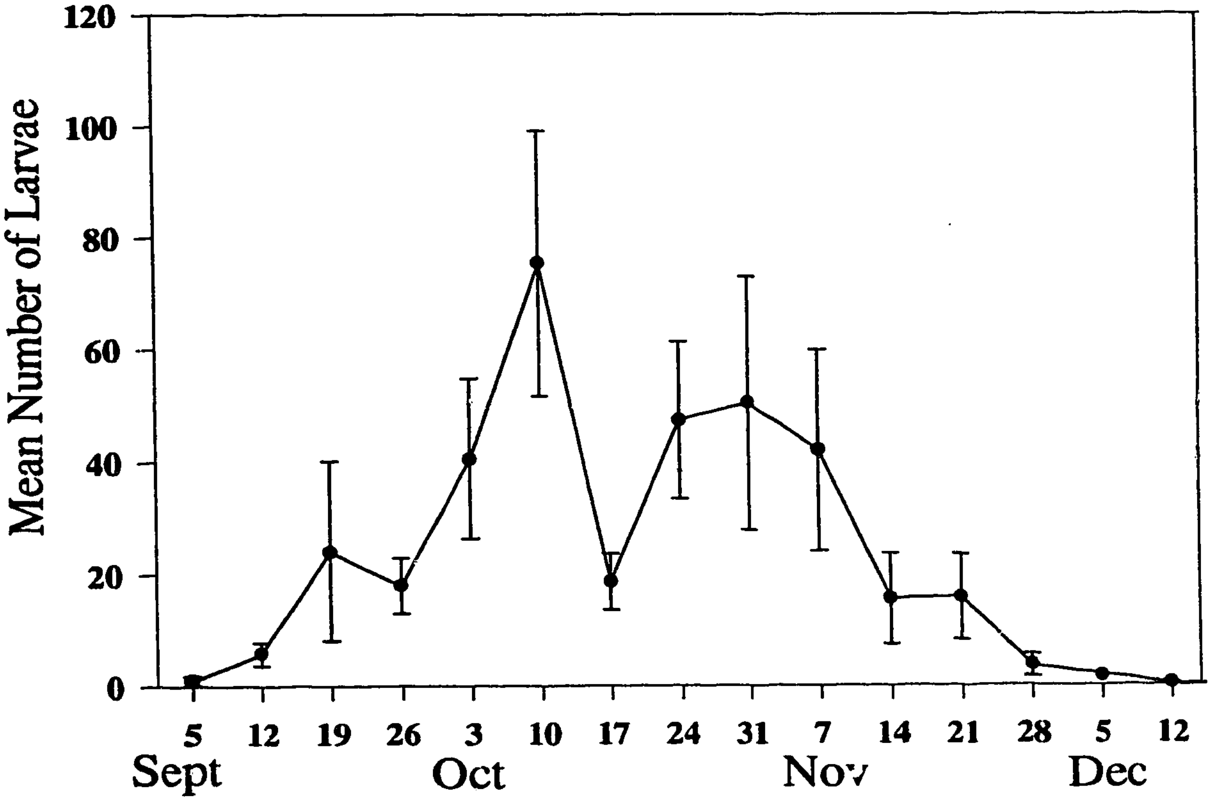
Habitat had a significant influence on larval tick density (F = 2.58, df = 4, P = 0.04) than did site. Because site had no effect on larval tick density, data from all sites and for October (period of larval tick abundance in EINP) were pooled for density analysis. Density of tick larvae differed among closed aspen, open aspen, grassland, shrubland and pooled habitats (F = 2.90, df = 4, P = 0.023). However, no differences in larval tick density between pair habitats were detected using Tukey's HSD multiple comparison test.

In both years, abundance and density of tick larvae were highest in closed aspen, open aspen, and shrubland (except labrador tea, but when pooled with other less encountered habitats, shows less abundance and density) (Table 2.5).

Larval tick abundance differed among September, October, and November 1992 (H = 44.42, P < 0.001) (Figure 2.5). Tick larvae were more abundant in October than in September (X^2 = 26.98, P < 0.025) or November (X^2 = 33.20, P < 0.025). There was no difference in larval abundance between September and November (X^2 = 0.56, P > 0.025). Overall, more tick larvae were collected in all time periods (except September 16 - 30) in 1992 than in 1991 (Table 2.2).

Density of tick larvae during the period September 18 to October 14 in 1991 did not differ from that of 1992 (t = 1.16, P = 0.247). However, density of tick larvae in some habitat types at some sites differed between 1991 and 1992 during the period. Density of larvae in willow bog at Site 4 was higher in 1991 than in 1992 (t = 2.15, P = 0.039) and density of larvae in shrubland at Site 4 was significantly higher in 1992 than

Figure 2.5 Mean number (abundance) of D. albipictus larvae collected in eight habitat types at Sites 1-4 in Elk Island National Park, September to December, 1992 (mean ± SE).


Mean Number of Larvae
120
100
80
60
40
20
0
5
12
19
26
3
10
17
24
31
7
14
21
28
5
12
Sept
Oct
Nov
Dec

in 1991 ($t = 1.97$, $P = 0.040$).

Longevity of tick larvae

Tick larvae lived longer in 1992 than 1991 (Figure 2.6). In 1992, larvae were found earlier and later in the aspen forest habitats. Larvae lived longer in the aspen forest habitats than in any other habitat (Table 2.6). Not only were very few larvae found in spruce forest and sedge bog habitats (Table 2.5), but they also lived for a very short time in these habitats (Table 2.6). Even though tick larvae were abundant in the labrador tea, longevity of larvae was relatively short (Table 2.6).

There was no pattern in mortality of tick larvae among the habitat types.

Weather and collection and survival of larval ticks

A snow storm accompanied by unseasonable cold on October 15, 1991 drastically reduced the number and lifespan of tick larvae in the park (Figure 2.7). Most tick larvae collected after the storm were dead (pers. observ.). Data on temperature, relative humidity, and wind, were not analyzed statistically because they were collected at different times during each day of flagging in the different habitats and sites. Thus, no comparisons were made among habitats and among sites even though differences in temperature and relative humidity among habitat types were recorded. However, the overall number of tick larvae collected in a day was influenced slightly by ambient temperature ($r = 0.06$, $P < 0.05$), but not relative humidity ($r = -0.03$, $P > 0.05$), or wind ($r = 0.02$, $P > 0.05$).

Figure 2.6 Total number of winter tick larvae collected during tick transmission seasons of 1991 and 1992, in Elk Island National Park, Alberta.

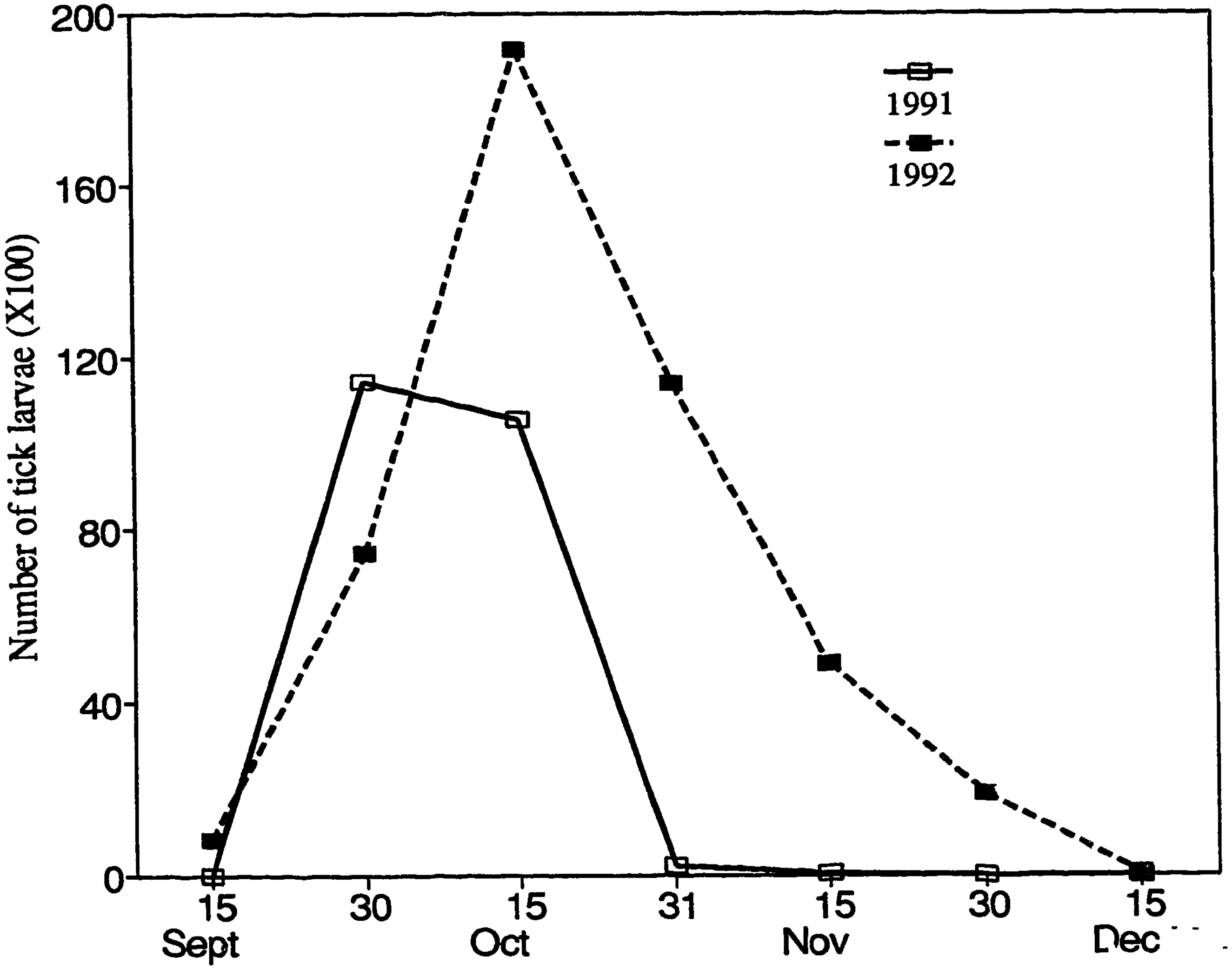

200
160
120
80
40
0
Number of tick larvae (X100)
1991
1992
15
Sept
30
15
Oct
31
15
Nov
30
15
Dec

Table 2.6 Longevity of *D. albipictus* larvae in eight habitat types during tick transmission season, Elk Island National Park, Alberta, 1992

Parameter	Habitat				Types			
	AC	AO	GR	LT	SF	SH	SB	WB
First larvae[1]	Sept 3	Sept 3	Sept 16	Sept 24	Oct 2	Sept 9	Sept 9	Sept 24
Dead larvae[2]	Sept 18	Sept 25	-[3]	Nov 12	-	Sept 26	-	Oct 15
Last larvae[4]	Dec 5	Nov 27	Nov 14	Nov 12	Oct 2	Nov 18	Oct 23	Nov 21
Longevity (days)[5]	103	85	59	49	-	70	44	58

[1] Date first larvae found.

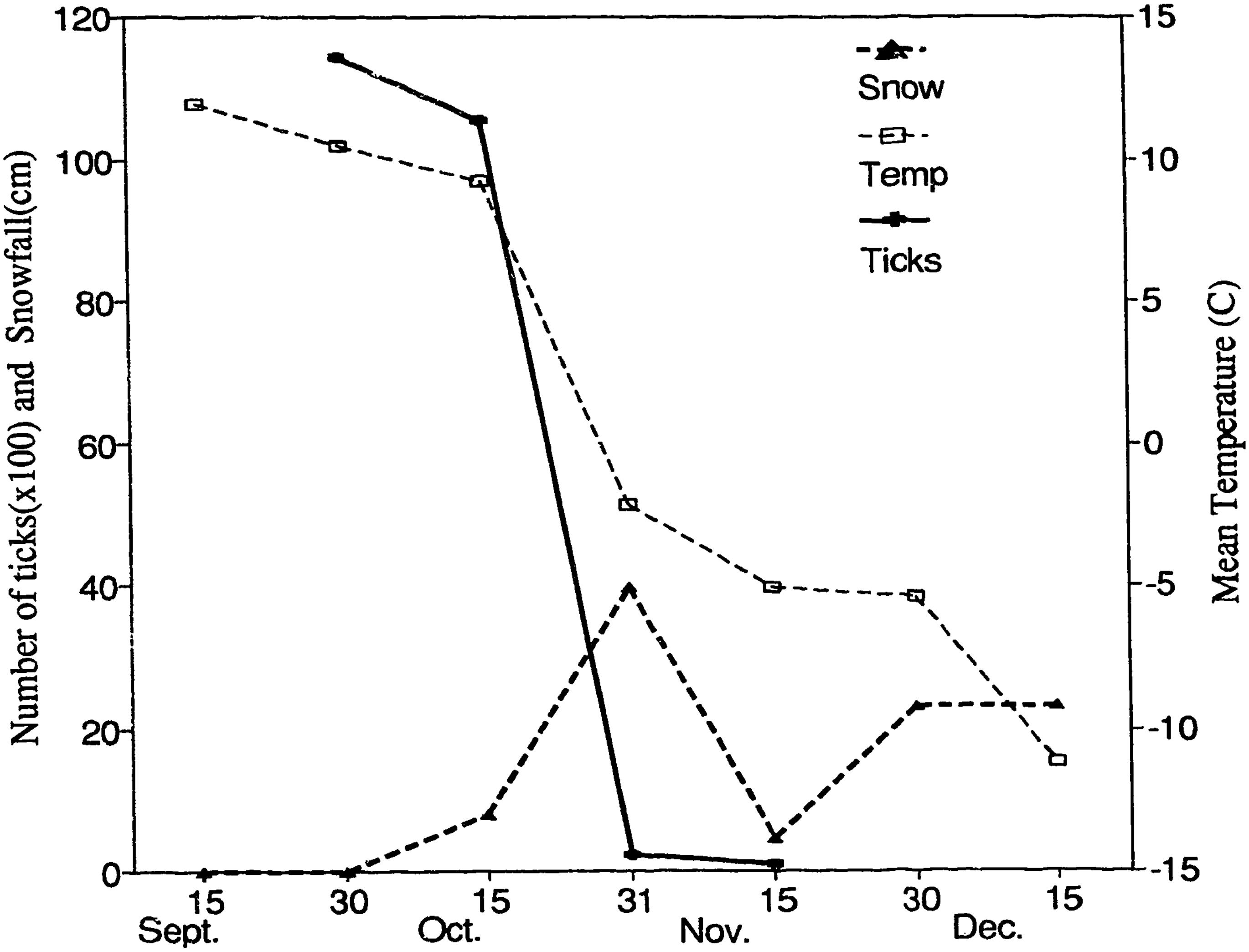
[2] Date first dead larva found

[3] No dead larvae found

[4] Last date on which larvae were found.

[5] Length of time live larvae were present.

Figure 2.7 Duration and number of winter tick larvae collected during 1991 tick transmission season in relation to snowfall and temperature in Elk Island National Park, Alberta.


120
100
80
60
40
20
0
Number of ticks(x100) and Snowfall(cm)
15
10
5
0
-5
-10
-15
Mean Temperature (C)
Snow
Temp
Ticks
15
Sept.
30
15
Oct.
31
15
Nov.
30
Dec.
15

DISCUSSION

Sampling intensity

The best time to start sampling for tick larvae in EINP is early September, the period larvae start to climb vegetation (Drew and Samuel 1985). The late start in 1991 and the interruption of sampling by snow storm in mid-October resulted in few samples for the year.

In 1991 and 1992, the number of sample units collected differed between days and among sites. These differences were attributed to: 1) distance of sampling site to nearest motorable park trail. Sampling periods were usually short at sites far from motorable park trail (*e.g.* Sites 1 and 3) and few sample units were collected; 2) variable distances between transects. Transects were selected at random and sampled in the sequence in which they were selected. Where distances between transects were far apart, few transects were run at the site because of longer shuttling distances between transects. 3) terrain and thickness of vegetation on the course of transects. Transects that passed on rough terrain (rugged, waterlogged) or through thick vegetation (tall hazelnut, tall willow, spruce forest) took a longer time to sample, resulting in few transects for the day and consequently few sample units being collected; 4) Change in daylight hours and weather conditions during the transmission season also affected sampling. Longer daylight period in early autumn (September), with sunset at 7:00 pm, resulted in sampling more transects and thus more sample units. In late autumn (November) daylight period was short and with sunset around 4:00 pm few transects and few sample units were collected in a day.

These obstacles either singly or in combination affected the number of samples collected at a site in a day. In all, fewer samples than projected were collected.

Though the recategorization of the vegetation types of EINP into eight habitat types for this study reflected physiognomic differences and consequently microclimatic differences among each other, the chances of encountering some habitat types were greatly reduced and some habitat types such as labrador tea, spruce forest, sedge bog and in some cases willow bog with low frequency of occurrence had to be pooled for some analyses. Spatial distribution of some habitat types in EINP are infrequent and when found, are so small in size that the microclimate within it is similar to the microclimate of surrounding larger habitat type. For example, similar temperatures and relative humidities were recorded in a small labrador tea bog and in an adjacent large willow bog. Much broader categorization of habitat types to increase frequency of encounter is suggested for future ecological studies of this nature in EINP.

Distribution, abundance and density of winter tick larvae

The differences in distribution, abundance and density of tick larvae detected among sites and habitat types in EINP in this study could be due to differences in many factors including moose density, topography, vegetation community structure and climatic conditions among sites; and moose density, moose habitat use and microclimatic conditions among habitat types. But only moose density among sites and habitat use by moose and microclimatic conditions among habitat types were addressed in this study.

Sites

Even though distribution and abundance of tick larvae differed significantly among sites, these differences could not be based solely on moose density because distribution and abundance of tick larvae in two of high moose density sites (Site 2 and 3) did not differ significantly from that of low moose density site (Site 4). Also distribution and abundance of tick larvae at Sites 2 and 3 were significantly different from Site 1 (another high moose density site). Several factors may be responsible for the outcome but only a few probable explanations are put forth here: 1) sample size differences between Sites 2 and 3 and Site 4. Probably there were not enough samples collected at Sites 2 and 3 to detect subtle differences in larval distribution and abundance that might exist between them and the low moose density site. Significantly more sample units were collected at Site 4 than either at Site 2 or Site 3 (Table 2.1); 2) moose movements at the sites. Because there were relatively few restrictions to movement at Sites 2 and 3 (only a perimeter fence to the east), unlike many restrictions at Site 1 (a perimeter fence to the north and west and a lake to the south), moose could move further than the site boundaries particularly during spring when moose are searching for food resources. Many investigators (Berg and Phillips 1974, Best et al. 1978, Risenhoover 1986, Cederlund 1989, Cederlund et al. 1989) have reported that moose movement and distribution can vary seasonally and from year to year depending on availability and accessibility of resources. It might be possible that moose moved beyond the site boundaries of Sites 2 and 3 during spring resulting in few engorged female ticks and consequently low abundance of tick larvae at these sites during autumn similar to a low moose density site;

3) some factors other than, or in conjunction with, moose density may be important in determining distribution and abundance of tick larvae in EINP. It may not be reasonable to attribute a phenomenon to a single factor. More study is needed to decipher the factors that affect tick reproduction in EINP; 4) high density of moose in EINP. Because of the high density of moose in EINP, they occur in most part of the Park. Therefore, few site differences in moose densities will exist and consequently no differences in larval distribution and abundance.

Moose density did not influence the density of tick larvae because the reproductive biology of female ticks, *i.e.*, number of eggs laid, egg development, success of egg hatch, and number of larvae, is influenced by weather factors and not the number of hosts present.

Strong evidence is lacking to conclude that moose density in EINP influenced the distribution and abundance of *D. albipictus* larvae, but host density has been reported to significantly influence the distribution and abundance of other species of ticks. High density of white-tailed deer , the main host, in some habitats in Oklahoma resulted in high numbers of *Amblyomma americanum* larvae and adults in the following summer and spring, respectively (Semtner and Hair 1973). Abundance of *I. scapularis* was greatly reduced when the density of white-tailed deer, its main host, was reduced (Adler et al. 1992).

Habitat types

Results of this study have shown that in EINP, where moose roamed most part of the Park, habitat type had more influence on distribution, abundance and density of winter tick larvae than site. One major difference among structurally different habitat types is the difference in microclimatic conditions. Differences in temperature among habitat types in EINP have been reported by Drew (1984). Distribution, abundance and density of tick larvae among habitat types therefore reflect, in part, the degree of suitability of habitat types to the survival and reproduction of engorged female ticks, being higher in habitats that are suitable and lower or absent in habitats that are not suitable (Semtner et al. 1971). Low distribution, abundance and density of tick larvae found in sedge bog and spruce forest strongly suggest that these habitats are unsuitable to female winter tick survival and reproduction in EINP. Closed aspen, open aspen, labrador tea and shrubland habitats, which showed high distribution, abundance and density of tick larvae in 1991 and 1992 appear to be suitable habitats for tick survival and reproduction and therefore important (except labrador tea) in winter tick transmission in the Park.

The high distribution, abundance and density of tick larvae in closed aspen, open aspen, labrador tea and shrubland could due to the following factors: 1) optimal microclimatic conditions in these habitats which resulted in higher survival of female ticks, better oviposition and eclosion of eggs. Daily ground level temperatures in closed aspen, open aspen and shrubland (see chapter 4) ranged between 15 - 20 °C during the reproductive period; *i.e.*, June - August, of winter tick in EINP. Lower and upper critical threshold temperatures for D. albipictus reproduction reported from laboratory experiments were 15.1 °C and 30 °C, respectively (Glines 1983). Drew (1984) also reported that 60% and 72% of engorged females laid viable eggs at 25 °C and 19 °C, respectively. While laboratory results should not be extrapolated to field conditions, they may help define an optimal range of temperature requirements in the field. Because temperatures within these habitats during the reproductive period fall within the laboratory range of optimal temperature conditions for winter tick reproduction, it is suggested that they also provided optimal conditions for winter tick reproduction in the field. The low distribution, abundance and density of tick larvae in spruce forest and willow bog may be because of the low temperatures in these habitats during the reproduction period of winter tick resulting in poor survival and reproduction of female ticks (Sutherst 1983); 2) Because host density influences tick abundance (Semtner and Hair 1973, Adler et al. 1992), it is suggested that moose selected closed aspen, open aspen, labrador tea and shrubland habitats during spring when female ticks were dropping from moose. More moose suggests more female ticks dropping in the habitat and subsequently abundant tick larvae in the habitat during autumn.

In EINP, moose prefer sedge bog and willow bog during spring (Appendix , Cool 1992, unpubl. report), as also reported in other parts of Alberta (Nowlin 1978), but few larval clumps and low abundance of larvae were found in these habitats. High moisture conditions were inimical to survival of female ticks in these habitats and thus reproduction efficiency was low (chapter 4). Even though studies show that closed aspen, open aspen and shrubland were selected less than sedge and willow bogs by moose during spring, it is still possible that many female ticks can drop in these habitats. Nobody really knows the mechanism and rate of female winter ticks disengagement though it has been observed that many female ticks drop from moose at moose "bedding"sites (W.M. Samuel 1994, pers. comm.). Most parasite species disengage when hosts are resting in dens, burrows and bedding sites (see review by Sousa and Grosholz 1991). Also, as moose walk through closed aspen, open aspen and shrubland habitats (which are vast in EINP) to the preferred sedge and willow habitats (which are isolated), many female ticks can drop in the former habitats and with the optimum microclimatic conditions in these habitats, abundant tick larvae can be found in autumn.

The mechanism of tick transmission in EINP may be similar between years because the ratio of larval tick abundance among habitat types was similar between 1991 and 1992. Also, the same habitats (labrador tea, closed aspen, open aspen, shrubland) showed high abundance of larvae in 1991 and 1992 (Figure 2.5). However, the high abundance of larvae in labrador tea overscores its importance in tick transmission in EINP. Labrador tea forms about 1% of EINP and was infrequently encountered during sampling (even though almost all those rare encounters resulted in large numbers of larvae), indicating similar chances of being traversed by moose during the transmission season. Though labrador tea may be a suitable habitat for female ticks survival and reproduction, it cannot contribute much to the number of tick larvae picked by moose during the transmission season considering the fact that all moose in EINP are infested with ticks with about 20% having over 50,000 ticks by winter (Samuel and Welch 1991). High abundance of tick larvae in closed aspen, open aspen and shrubland, and the fact that those habitats together form almost 70% of EINP, suggest that those are the most important habitats for winter tick transmission in EINP.

The low abundance of tick larvae in sedge bog and willow bog during autumn was attributed to poor survival of female tick due to water-logging and cold temperatures in these habitats during spring and some part of summer (chapter 4). Low abundance of tick larvae in spruce forest was due either to spruce forest not being selected by moose during spring probably because there is little food or the long period of low temperatures and high relative humidities in spruce forest reduced female tick survival and reproduction (see chapter 4).

Transmission period and year

Differences in abundance of tick larvae between September, October and November, 1992 were attributed to timing of climbing of vegetation, transmission and mortality of tick larvae. Because tick larvae start climbing vegetation in early September (Drew and Samuel 1986), few larval clumps were collected at the beginning of September affecting the overall total of tick larvae collected for September. By October, almost all tick larvae were on vegetation and with few mortality, many tick larvae were collected. In November most larvae would have attached to hosts and some would have died from bad weather and old age resulting in few larval clumps on vegetation; thus so few tick larvae were collected.

The high abundance of tick larvae in October coincides with the breeding season of moose (Lent 1974, Stelfox and Stelfox 1993), a period when moose are very active in courtship. Synchrony of high abundance of tick larvae, high activity of larvae, and high activity of moose during October suggests that peak transmission of winter tick larvae in EINP occurs in October. The results of this study suggest that winter tick abundance in EINP may be similar between years except during periods of epizootic. However, high abundance of tick larvae may shift from one habitat type to another habitat type or from one site to another site between years because microclimatic conditions favorable for adult female winter tick survival, oviposition and eclosion of eggs in a habitat could differ between years. Also, host habitat selection pattern, dictated by relative availability and abundance of food resources, could also differ between years. A shift in high larval tick abundance among habitat types at a site between years was also observed by Adler et al. (1992).

Sampling technique

The standard tick-drag (flagging technique) was used in this study to collect tick larvae in different habitat types that occur at random along a transect. The flagging technique has the advantage of providing immediate results and many samples can also be collected over a large area in a short period of time. Choice of a sampling method for collecting ticks usually depends on the species and life stage of the tick, the season of the year, climatic conditions, topography of the area and the purpose of the study (Wilkinson 1961, Sutherst et al. 1978, Ginsberg and Ewing 1989). Many workers (Wilkinson 1961, 1967, Semtner and Hair 1973, Drew and Samuel 1985, Randolph and Steele 1985, Ginsberg and Ewing 1989, Daniels and Fish 1990, Harlan and Foster 1990, Lane and Stubbs 1990, Spickett et al. 1991, Falco and Fish 1992) have used the tick-drag technique to collect many species and life stages of ticks. The efficiency of flagging, which depends on the habitat type (Wilkinson 1961), was not assessed prior to sampling in 1991 and 1992 because Drew and Samuel (1985) had already reported an overall 16% efficiency of flagging in EINP. Modification to the standard tick-drag is usually necessary to improve flagging efficiency for free-living ticks. Modified tick-drags have been used to collect immature I. scapularis, nymphal H. leporispalustris and all stages of A. americanum (Siegel et al. 1991, Carroll and Schmidtmann 1992), and I. pacificus (Smith 1990). Modification of the standard tick-drag for this study would have improved flagging efficiency in some but not all the habitat types because of the structural differences between each other.

Many authors have also used host trapping and examination technique (Pinger et al. 1991, Alder et al. 1992, Falco and Fish 1992, Mannelli et al. 1993, Smart and Caccamise 1988, Ai et al. 1991, Westron et al. 1985, Estrada-Pena et al. 1990, Schulze et al. 1984, Luckhart et al. 1991, Richerson et al. 1992) and carbon dioxide (CO_2)-baited trapping technique (Wilson et al. 1972, Koch and McNew 1982, Gray 1985, Anderson and Magnarelli 1980, Ginsberg and Ewing 1989, Falco and Fish 1989, 1991, Solberg et al. 1992, Semtner and Hair 1975) to collect many species and life stages of ticks. These two methods were inappropriate for this study.

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CHAPTER THREE

QUESTING BEHAVIOR, HEIGHT DISTRIBUTION AND ORIENTATION OF WINTER TICK LARVAE ON VEGETATION IN ELK ISLAND NATIONAL PARK, ALBERTA.

INTRODUCTION

Finding a vertebrate host is essential to survival of ticks. To accomplish this, some ticks ascend vegetation and 'ambush' a host as it passes by (Barnard 1991, de Castro 1991). They become stimulated to quest (*i.e.*, wave their forelegs in the direction of a host stimulus) by the presence of vertebrate hosts.

One such ambushing tick is the winter tick, Dermacentor albipictus, an important pest of moose (Alces alces) (Samuel and Welch 1991). In Alberta, larvae of the winter tick ascend vegetation in early September, form aggregations (hereafter called clumps) and wait for contact with a passing host (Wilkinson et al. 1982, Drew and Samuel 1985). Details of the ambushing phase of this life cycle are incomplete, but larvae survive in clumps on vegetation for several months. Once on vegetation, larvae remain there until they either transfer to a host, are blown off, buried by snow or die (Drew and Samuel 1985, Samuel and Welch 1991).

Diurnal and seasonal activities of ticks play an important role in determining success in finding a host (Sutherst et al. 1978, Loye and Lane 1988, Gray 1991). Meteorological factors such as temperature, moisture, light, wind and day length affect these activities and survival (McEnroe and McEnroe 1973, Nosek 1978, Gary 1985, Harlan and Foster 1986, 1990, Loye and Lane 1988). Samuel and Welch (1991) found that weather affected survival of clumps of D. albipictus on vegetation. Numbers of clumps decreased following rain with accompanying wind and snowfall.

OBJECTIVES

The present study was designed to quantify the behavior and distribution of winter tick larvae on vegetation in Elk Island National Park (EINP). Specific aims were:

1) to determine questing of winter tick larvae in relation to temperature, relative humidity and wind;

2) to determine vertical distribution of clumps of larvae on vegetation under natural conditions, and ;

3) to determine the influence of wind on location of clumps of larvae on vegetation.

METHODS

Questing behavior

Winter tick questing behavior was studied at two sites in EINP. The first site was a wooded habitat of young aspen (Populus spp.) in which a tick-infested moose had died in spring 1992, and some larvae were found at the carcass site in autumn 1992. This habitat was similar to closed aspen (see chapter 1, p. 16) except that saplings were equal to or less than 4 m tall and about 3 cm diameter at breast height (dbh). Observations were made weekly from September 28 to December 7, 1992.

The second site was a shrubland with hazel (Corylus cornuta) and shrubs less than 1 m tall. It was seeded in spring 1992 with engorged female ticks collected from a dead moose. Observations were made weekly from October 12 to November 23, 1992.

Time of observation varied between days but was usually between 0900 and 1200 hrs in the aspen habitat and between 1300 hrs and 1500 hrs in the shrubland habitat on the same day. Clumps of larvae chosen for observation were about 5 m from each other so that presence of the observer at one clump would not initiate questing of a nearby clump. On each visit to each site, larvae in separate clumps were stimulated with warm breath and the time taken (response time in sec) for about one-third of the larvae on the outer surface of a clump to start questing was recorded using a stopwatch.

From 4 to 10 clumps were observed on each visit to each site. Only clumps in which larvae were inactive on approach were chosen for observation. Each clump chosen was exposed to warm breath from a distance of about 15 cm for approximately 2 sec. Then larvae were observed from a distance of about 30 cm. If larvae were not questing after about 20 seconds, they were exposed to a second breath of warm air. At low temperatures (≤ -10 °C), more than two breaths were used to activate tick larvae. At each observation, temperature and relative humidity were measured at about 1 m above ground with a hand held HM 34 Temperature and Humidity Indicator (Vaisala Instruments, Helsinki, Finland). Wind intensity was determined subjectively as strong (>20 kph), mild (10-20 kph) or nil (<10 kph). Wind direction, with reference to True

North determined by a Ranger Magnetic Compass (Silva Company, Stockholm, Sweden), was also recorded.

Vertical height distribution

Height of clumped larvae on vegetation (soil surface to middle of clump) was recorded only in the young aspen habitat. Clumps were sampled opportunistically as they were encountered. Measurements were taken on September 15 (n = 10 clumps), October 19 (n = 23) and November 16 (n = 19), to coincide with the beginning, middle, and end of the winter tick transmission period, respectively. If two clumps were found on the same piece of vegetation, only the height of the higher clump was measured in order to avoid the influence of a single tree or twig on the heights of larvae at the site. The height of wooded vegetation (mainly aspen) at the site was measured on November 30, 1992, to determine the maximum height available to tick larvae at the site.

Orientation of larvae on vegetation

Measurement of the orientation of tick larvae on vegetation was done in the young aspen habitat. Locations of clumps of larvae on vegetation were determined with reference to True North (0°). Only clumps on vertical vegetation were selected because larvae under more horizontally arrayed twigs or leaves did not show obvious orientation with regards to True North. Observation and recording of positions of larvae were made weekly from September 5, to November 16, 1992. The positions (direction of location) were assessed at the time larvae were inactive and the focal point (point of highest aggregation) of the clump was taken as the position of the clump on vegetation.

DATA ANALYSIS

Data were analysed using SYSTAT statistical analysis software (Wilkinson 1990) on a PC computer. Pearson correlation tests were used to examine the relationships between response time of larvae (from inactivity to questing) and temperature, relative humidity and wind and duration of the transmission season. Stepwise forward multiple regression analysis was performed to clarify and describe the interactive relationship of each of the weather factors with response time.

Mean height (± 1 standard deviation) of larval clumps on vegetation was determined for September, October and November and compared among these months using the Kruskal-Wallis test. The null hypothesis of no effect was rejected when $P \leq 0.05$. Mean temperature, relative humidity and wind conditions were also compared between the months.

Mean angle, median angle, and modal angle of orientation, and the range and dispersion were calculated according to Zar (1984).

RESULTS

Questing behavior

Human breath stimulated winter tick larvae to quest. After a human breath, larvae at the surface of clump were the first to start waving their forelegs. Larval response time was negatively correlated with ambient temperature (r = -0.84, P < 0.001) (Figure 3.1) being longer at low temperatures than at high temperatures. It took more than one stimulation of warm breath to activate larvae below 0°C. Response time was much longer even after more than two bouts of warm breath at -10°C or lower (Figure 3.1). Time from inactivity to questing by tick larvae was positively correlated with the progression of the transmission season (r = 0.77, P < 0.001) (Figure 3.2), relative humidity (r = 0.24, P = 0.009) and wind (r = 0.22, P = 0.015). Also, progression of the season was negatively correlated with temperature (r = -0.77, P < 0.001) and relative humidity (r = -0.59, P < 0.001).

Stepwise forward multiple regression analysis showed that temperature, relative humidity, progression of the season and wind were predictors of response time of larvae and that their influence on response time was highly significant (F = 169.711, P < 0.001). Time of day did not affect response time of tick larvae. Temperature played a greater role in influencing response time (std. coef. = -0.83, P < 0.001) than relative humidity (std. coef. = -0.38, P < 0.001), progression of the season (std. coef. = 0.34, P < 0.001) and wind (std. coef. = 0.09, P = 0.031). Response times were similar in the shrubland.

The number of larval clumps observed at the aspen site increased steadily from late September to mid-October and then steadily decreased to none by early December (pers. observ.).

Figure 3.1 Time (mean) from inactivity to questing by D. albipictus larvae following exposure to human breath at various ambient temperatures in a stand of young aspen habitat, Elk Island National Park, Alberta.

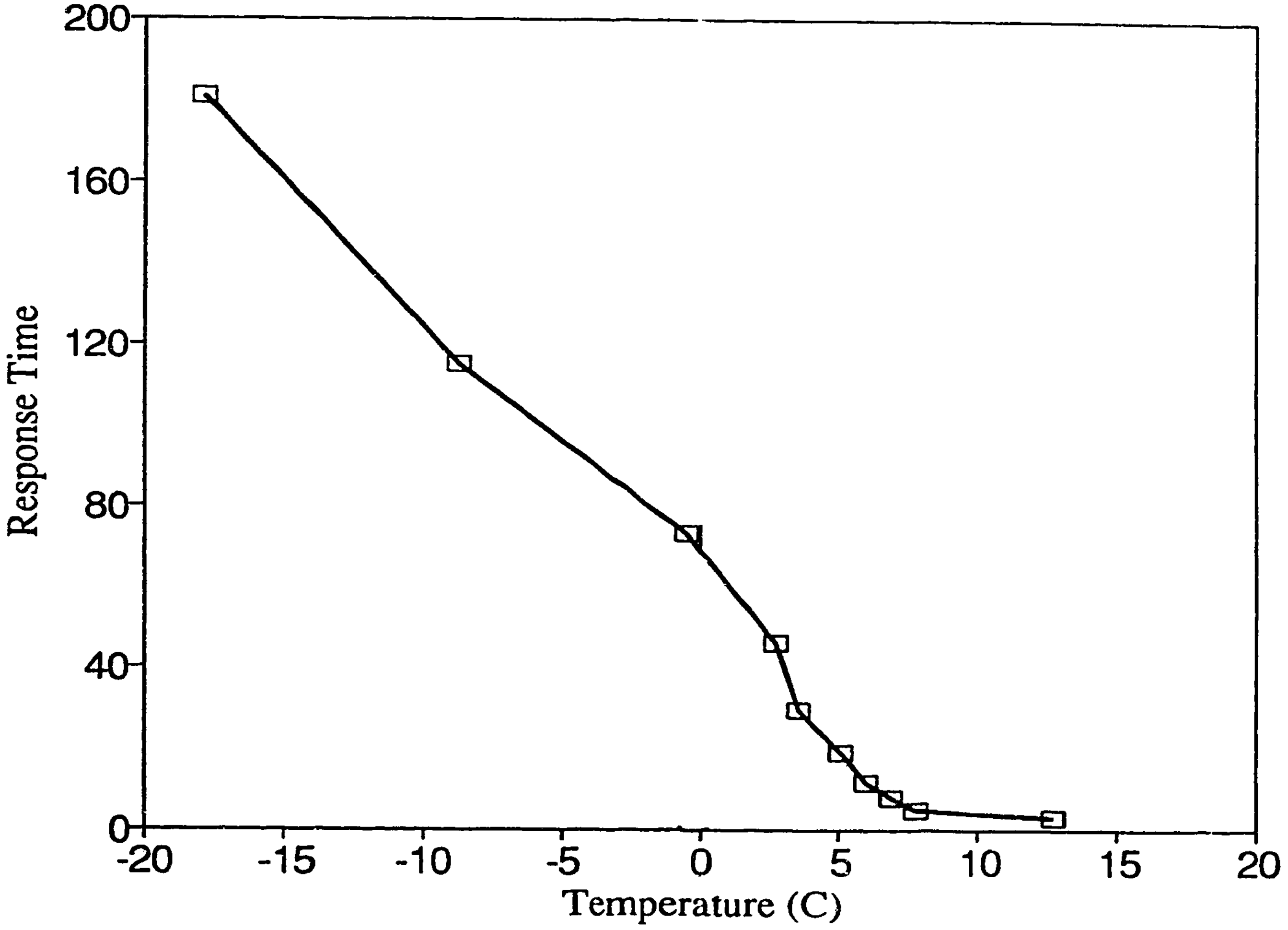
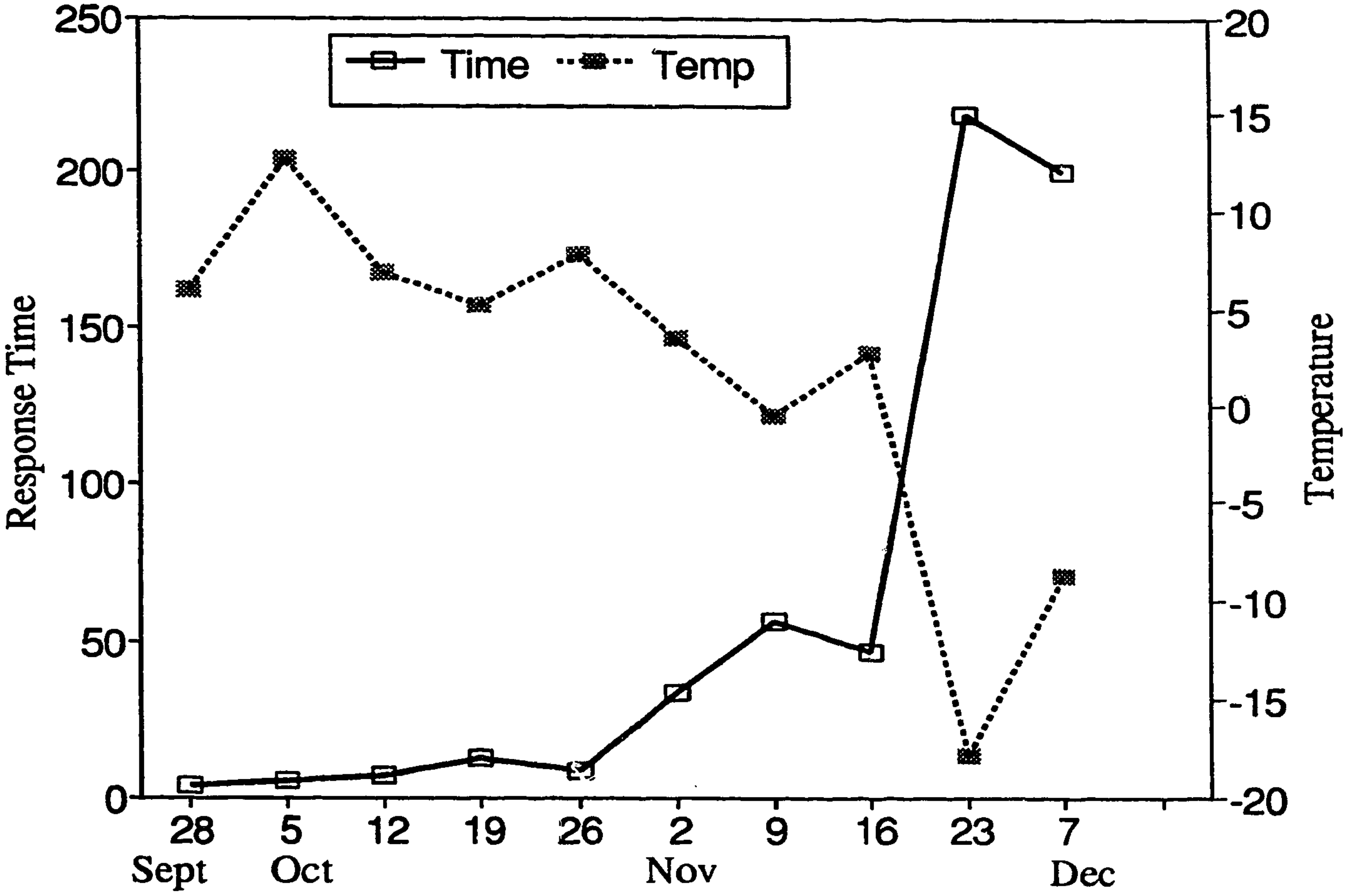

200
160
120
80
40
0
Response Time
-20
-15
-10
-5
0
5
10
15
20
Temperature (C)

Figure 3.2 Time (mean) from inactivity to questing by D. albipictus larvae following exposure to human breath, 28 September to 7 December 1992, in a stand of young aspen, Elk Island National Park, Alberta.


Time
Temp
Response Time
Temperature
250
200
150
100
50
0
20
15
10
5
0
-5
-10
-15
-20
28
Sept
5
Oct
12
19
26
2
Nov
9
16
23
7
Dec

Vertical height of clumps of larvae

The mean height of 52 clumps of larvae on vegetation did not differ significantly (H = 3.19, df = 2, $P < 0.001$) between the beginning (95.2 ± 36.1 cm), middle (122.5 ± 44.6 cm) and end (119.0 ± 37 cm) of the transmission season. The overall mean height was 116.0 ± 41.0 cm (range, 47 - 203 cm) (Figure 3.3). Thirty-one of 52 clumps were at heights lower than the maximum height of the vegetation on which the clumps were formed. The mean height of young aspen saplings at the site was 368.3 ± 34.0 cm.

Orientation of larvae on vegetation

All clumps (n = 43) formed on the leeward side of prevailing wind. Prevailing winds, which were either mild or strong, blew from the north-west (315°) during periods of observations throughout the duration of the study. However, EINP also experiences very mild persistent winds from the south (Olson 1985). Larval clumps were located on stems of vegetation from 22.5° clockwise to 180° but not on the west side of vegetation. Range of dispersion was 157.5°. Mean angular position of location of larval clumps was 84° ± 16°. The modal and median positions were 90° and 135° respectively (Figure 3.4). Dispersion of larval clumps was highly concentrated (r = 0.756) (*i.e*, clumps were not widely dispersed) (1 - r = 0.244) indicating a preference of location .

Because position of clumps of larvae on vegetation did not change on both bright and cloudy days, or with change in the position of the sun, it was inferred that solar radiation was not as important as wind in influencing the location of tick larvae on vegetation.

Figure 3.3 Frequency distribution of height of clumps of D. albipictus larvae on vegetation in a young aspen habitat in Elk Island National Park, Alberta.

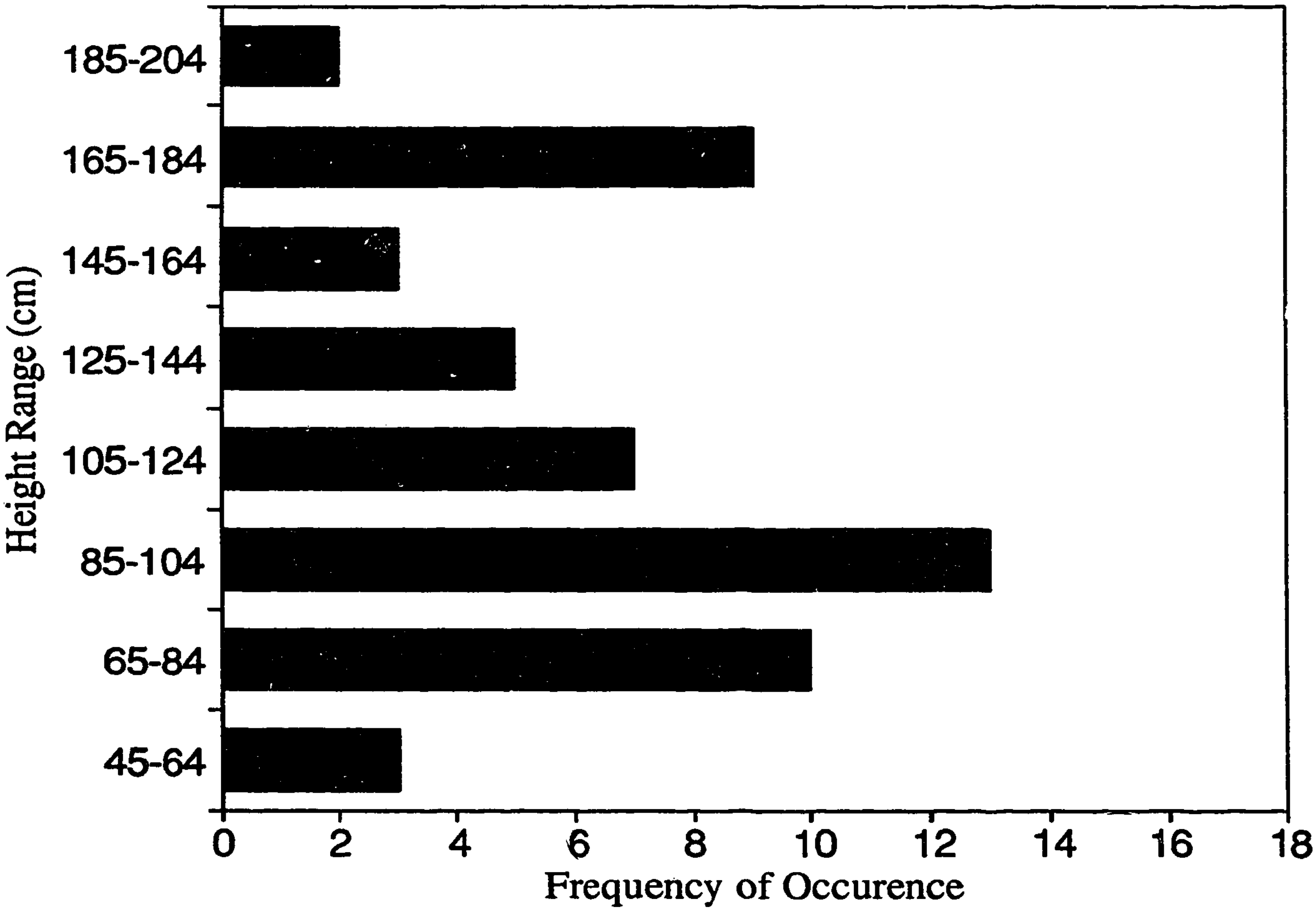
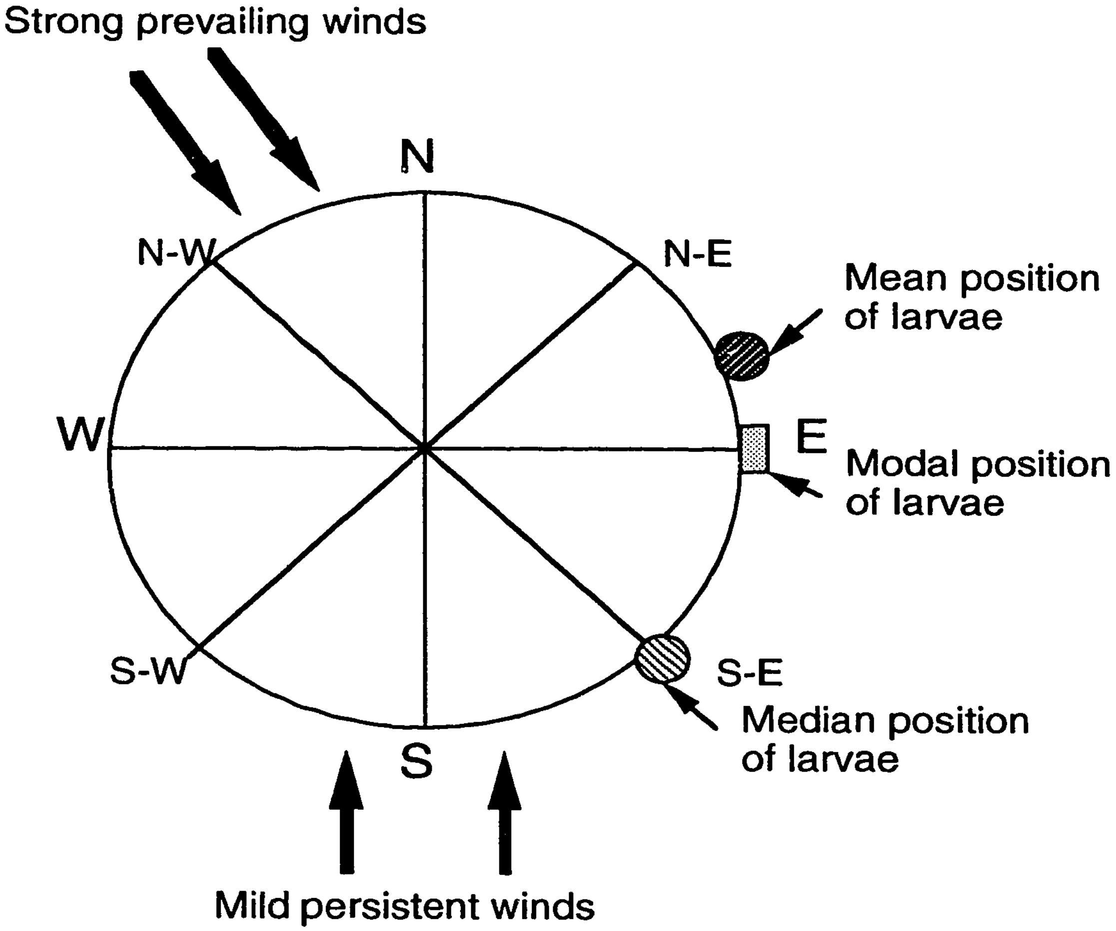

Height Range (cm)
185-204
165-184
145-164
125-144
105-124
85-104
65-84
45-64
0
2
4
6
8
10
12
14
16
18
Frequency of Occurence

Figure 3.4 Position of winter tick larvae on vegetation in relation to wind direction in young aspen habitat in Elk Island National Park, Alberta.


Strong prevailing winds
N
N-W
N-E
Mean position of larvae
W
E
Modal position of larvae
S-W
S-E
Median position of larvae
S
Mild persistent winds

DISCUSSION

Questing behavior

A clump of winter tick larvae contains from very few (<20) to several hundred individuals (personal estimate). It appears that legs of larvae in clumps are intertwined (pers. observ.), probably to assist in holding the clump together and to facilitate mass transfer to a host. Larvae in a clump are stimulated to quest by a variety of host-related stimuli such as odor, vision, vibration and radiant heat (Barnard 1991). During questing, legs disentangle and small aggregations of larvae fall from the clump (pers. observ.). If the passing host walks by or stops near the clump, it is probable that most, if not all, larvae can attach. Whatever the mechanism, it must be efficient because all moose in EINP appear to become infested annually and 20% of moose have at least 50,000 winter ticks each by winter (Samuel and Welch, 1991).

Ticks, as ectotherms, depend on an external source of heat energy for physiological and behavioral activities. A decline in ambient temperature reduces over all metabolism of ticks, thus restricting these activities and ultimately arresting activity at a critical low temperature (McEnroe 1977, Daniels et al. 1989, Duffy and Campbell 1994). Such temperature dependent activity has been shown for other arthropods (see review by Block 1990). The inference is that ticks quest within a range of optimum weather conditions, particularly that related to temperature. Results here indicate that temperature is more important than relative humidity and wind in determining questing by winter tick larvae. Similar observations were made by Duffy and Campbell (1994) on adult Ixodes scapularis. Temperature and relative humidity have been shown to influence questing behavior of other tick species (Nosek 1978, Gray 1985, 1991, Loye and Lane 1988, Harlan and Foster 1986, 1990).

The positive correlation between response time and progression of the transmission season, even when the effect of temperature was removed, is attributed to aging of the larvae. As tick larvae age, their energy reserves are reduced, some having been used for physiological processes. Also, questing is an energy expending activity that might be repeated many times during the life of the larvae. As energy stores are depleted, so too is the ability of larvae to respond to host stimuli. Other tick species have shown similar reduction in activity with age due to depletion of energy reserves (Lees and Milne 1951, Gray 1985, 1991, Steele and Randolph 1985) or reduction in moisture in the atmosphere (Fleetwood and Teel 1983).

The ultimate result of decreasing ambient temperature and larval aging is a decrease in transmission of ticks from vegetation to moose in late October and November. This does not mean that all transmission occurs in the active 'ambushing' sense. Dead larvae are found on flannel samples swept across vegetation in November in EINP (chapter 2) suggesting that living, inactive larvae can also catch-on to passing hosts that brush against vegetation. This form of transmission might be important during years of early cold weather that occasionally occurs in the north (*e.g.* October 1991).

The period of quick response time by larvae to host stimuli in late September and October (Figure 3.2), coincides in part to the mating season of moose (late September to mid-October) (Lent 1974, Stelfox and Stelfox 1993). During this time, rutting males chase females and, in the process, cover large areas of potentially tick-infested habitat. Synchrony of active larvae and active moose may be an adaptation for transmission of winter ticks in Canada and northern United States where optimal weather conditions in autumn can be short.

Vertical height of clumps

If distribution of tick larvae in habitat is important for transmission (chapter 2), so too is the position of larval clumps on vegetation. Results of the present study confirmed some previous findings of Drew and Samuel (1985). Clumps usually form at variable heights off the ground at or near the tips of vegetation. That position remains unchanged during the transmission season suggesting that tick larvae do not make diurnal vertical migrations. This is unlike many tick species that clump to facilitate host acquisition and also migrate to the litter periodically to replenish body water lost while exposed to dry air at the tips of vegetation (McEnroe and McEnroe 1973, Steele and Randolph 1985, Koch 1988, Garris and Popham 1990, Gray 1991).

One complicated question is whether or not winter tick larvae in EINP form clumps at heights corresponding to that of their usual hosts, moose, elk, and deer. Many ixodid ticks appear to do this, thus maximizing chances for contact with their host (Sonenshine and Stout 1968, Rechav 1978, Randolph and Steele 1985, Barnard 1989, 1991). Mean chest height at the brisket of adult moose, elk, and deer (measurements of animals in EINP) are approximately 105, 89, and 64 cm, respectively (Telfer and Kelsall 1979). The fact that more clumps were found at the height range 85-104 cm and 45-84 cm compared to six other ranges might reflect actual selection of the heights similar to that of available hosts.

Orientation of larvae on vegetation

Clumps of winter tick larvae appear to avoid direct contact with wind. In Edmonton, during autumn, strong winds, averaging about 20 kph, generally blow from the north-west sector while some persistent winds blow from the south (Olson 1985). The fact that no clumps were found on the west side of twigs suggests that larvae choose the aspect shielded from the effect of the strong winds. This is in agreement with the observation that winter tick larvae are found amongst protective awns of grasses or crevices of twigs during strong wind and only emerge when they scent host stimuli (Samuel pers. obs.). Samuel and Welch (1991) found that wind and snow in mid to late October accounted for sharp declines in number of clumps of D. albipictus larvae on vegetation in central Canada.

The effect of wind on the orientation of other tick species has been documented. Lees and Milne (1951) reported that wind direction had a significant effect on the orientation of larval Ixodes ricinus on vegetation. Although solar radiation did not appear to be important in orienting host-seeking D. albipictus, in present study, it has been reported as important in orienting Dermacentor variabilis (Atwood and Sonenshine 1967) and adult Amblyomma americanum (Semtner and Hair 1973) on vegetation.

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CHAPTER FOUR

SURVIVAL AND OVIPOSITION OF ENGORGED ADULT FEMALE WINTER TICK, *DERMACENTOR ALBIPICTUS* (ACARI: IXODIDAE), IN CONTRASTING HABITAT TYPES IN ELK ISLAND NATIONAL PARK, ALBERTA.

INTRODUCTION

There are many field studies on the biology of ticks (e.g., Branagan 1973, Patrick and Hair 1979, Koch 1983, Dipeolu 1985, Garris et al. 1990, Spickett and Heyne 1990), but few have addressed the effect of habitat. Garris et al. (1990) reported higher mortality of female ticks and eggs in grass habitat, which had lower relative humidity and higher temperatures ($\geq$ 30 °C), than wooded habitat. Overall, more female ticks laid eggs and more eggs hatched in the wooded habitats than in grass habitats. These field studies have been done in basically equatorial or southern North Temperate climates with only a few studies done in northern regions. The few northern studies deal mainly with Dermacentor albipictus (Drew and Samuel 1986, Zarnke et al. 1990). Knowledge of the biology of ticks under natural conditions is important for use in conjunction with control measures to eradicate ticks. Several field studies (Hugh-Jones 1991, Teel 1991, Randolph 1993) have identified key habitats that provide optimum conditions for the reproduction of ticks thus enabling predictions of tick distribution and population size in locales and, recently, in broad geographic regions

At Elk Island National Park (EINP), engorged females of D. albipictus drop from moose in various habitat types during spring to reproduce in summer. The study was designed to evaluate more closely the suitability of the various habitat types of EINP for female winter tick survival and reproduction.

OBJECTIVES

The main objective of this study was to assess the influence of eight habitat types on the survival and oviposition of adult female D. albipitus, egg eclosion and longevity of tick larvae under field conditions.

METHODS

Sites were selected opportunistically from eight physiognomically different habitat types located along the main park road between Tawayik Lake intersection and the Park Headquarters (see Figure 2.1). Areas selected for the experiment were parts of typical stands of the following habitat types: closed aspen (AC), open aspen (AO), grassland (GR), labrador tea (LT), spruce forest (SF), shrubland (SH), sedge bog (SB) and willow bog (WB) (see chapter 1 for details). The open aspen habitat in this study was the site of an old burn. It had lower density of trees than the 'typical' open aspen habitat described in chapter 1. In terms of canopy cover, density of trees, shading, etc., open aspen, grassland, shrubland and sedge bog were considered 'open' while closed aspen, labrador tea (because of similar microclimate with surrounding habitats), spruce forest and willow bog were considered 'closed'.

On April 24, 1992, engorged adult female D. albipictus were recovered from a dead moose found near the Park Headquarters. The ticks were left overnight in a paper box near the dead moose to maintain the influence of field conditions on ticks. On April 25, 1992, the engorged female ticks were placed individually in 4 cm^2 organza gauze bags of fine mesh (27 um). The bags were sealed using a candle flame. Ticks could be seen through the mesh of these bags. Similar bags were recommended by Sutherst et al. (1978) for field studies of ticks. Studies have also shown that ticks survive in this type of bag as well as they do in standard "rearing" vials (Koch 1984).

Twenty-three bags of ticks were selected randomly from the paper box for placement in each of the eight habitat types. In all but sedge bog habitat, five to six individual bags of ticks were placed in each of four circular wire gauze cages (0.3 m^2) driven about 3 cm into the ground (Koch 1984, Drew and Samuel 1986). The cages prevented predation by birds and mice. Cages were located about 5 m apart. Bags were labelled and placed on the soil surface beneath approximately 2 cm of litter. Sedge bog was water-logged at the time of tick release so five to six bags of ticks were placed at four different spots submerged in water.

Bags of engorged female ticks in the different habitat types were not disturbed from April 25 to May 24, 1992. From May 25 to July 4, and then weekly from July 10, to August 7, 1992, bags of engorged female ticks were temporarily removed from their cover every other day to determine survival of engorged female ticks, onset of oviposition and death of oviposited females. Dead ticks were identified by their dark brown and pink color under dry and water-logged conditions, respectively. The day of death or day of oviposition of an engorged female tick was taken as the day prior to the day of detection.

Survival of engorged female ticks, preoviposition period, oviposition period and longevity of oviposited female ticks (hereafter referred to as lifespan) in the different habitat types were determined from the above recordings.

Survival of female ticks was estimated as the number of engorged female ticks that survived in a habitat type to lay eggs. Preoviposition period was the number of days from when a female tick was put out into the field to when the first egg was laid (Campbell and Harris 1979, Addison and Smith 1981). Oviposition period was the number of days from when the first egg was laid to when the last egg was laid. The last day of oviposition was taken as the day before the death of an ovipositing female tick. Most ixodid ticks die a day or two after laying their last batch of eggs (Sweatman 1967). The lifespan of oviposited female ticks was estimated as the period from the day female ticks were put in the field to the day of death.

After oviposition, bags of eggs were removed temporarily from litter every other day from August 10 to September 7, 1992, and observed to determine eclosion date and establish incubation period for eggs in each habitat type. Incubation period was the number of days from when first egg was laid to when first larva hatched (Drew and Samuel 1986).

Temperature and relative humidity were measured at about 2 cm above ground using a hand-held Temperature and Humidity Indicator (Vaisala Instruments, Helsinki, Finland) during each time of observation from May 25 to September 7, 1992.

No eggs hatched after September 3 (pers. observ.). On September 13, 1992 two bags of tick larvae with eggs from grassland, labrador tea, spruce forest and willow bog and four bags from closed aspen, open aspen and shrubland were collected to determine the number of unhatched eggs, live larvae and dead larvae. All remaining organza gauze bags of larvae (and unhatched eggs) were suspended, about 1 m above ground, on vegetation nearest to the cages with a piece of biodegradable cotton thread in all habitat types. Two bags of tick larvae with eggs were collected weekly or bi-weekly in each habitat (*i.e.*, on September 28, October 12, 19, 26, November 2, 16 and 30, 1992) and treated as above. Temperature and relative humidity at the level of the organza gauze bags (*i.e.*, about 1 m above ground) were measured in each habitat type at the time bags of larvae and unhatched eggs were collected.

In the laboratory at University of Alberta, the bags of tick larvae with eggs were opened and placed in a black, opaque, kodak film vial with an organza guaze cap of fine mesh to allow light into vial. Live tick larvae climbed to the top of the vial in response to light and were consequently separated from the dead tick larvae and eggs. Live larvae were counted under an illuminated magnifying glass. Dead larvae and eggs were preserved in 70% alcohol and counted under a dissecting microscope at the end of the field season.

DATA ANALYSIS

Data were analyzed using SYSTAT 5.0 software (Wilkinson 1990) on a personal computer. Mean values of survival and reproductive parameters of the female ticks were summarized by habitat type. Survival of female ticks among habitat types was evaluated by comparing number of dead to live female ticks using a G test. Kruskal-Wallis tests were performed to compare differences in mean pre-oviposition period, oviposition period, incubation period, lifespan of oviposited female ticks, number of eggs laid, number of larvae and percent eclosion among the different habitat types. Assumptions of homogeneity of variances of the above variables were not satisfied (even with transformed data) for ANOVA tests. The null hypothesis was rejected at an alpha level of 0.05. Where an overall Kruskal-Wallis test indicated significant difference among habitats in any of the above parameters, pairwise Mann-Whitney comparison tests were done to detect groups that differed. Where each group was compared with $\underline{n}$ other groups, result of the individual test was accepted as significant if only $P \leq 0.05/\underline{n}$ for the individual test.

Mean temperature and relative humidity data, recorded between 0900 to 1300 hr in the different habitat types for three time categories namely June, July, August, were summarised by habitat type. All five temperature and relative humidity recordings in May were made after 1300 hrs and so were not included in the summary.

Longevity of tick larvae in each habitat (expressed as percentage of live tick larvae at a particular period of time) was estimated for four time periods (between September 13 to November 30) that corresponded to the beginning of the experiment, one month later (peak transmission period of tick larvae in EINP), two months later, and at the end of the experiment (end of active transmission of tick larvae in EINP). Because longevity of tick larvae at each time period was similar among the 'closed' habitats and among 'open' habitats, longevity data were pooled in each group. Longevity was then compared between 'closed' and 'open' habitats. Mean temperature and relative humidity were summarized for ‘closed’ and ‘open’ habitats.

RESULTS

In general, habitats with canopy cover (*i.e.*, the ‘closed’ habitats) were colder and more humid, in June, July, and August, than the habitats with less cover (*i.e.*, the ‘open’ habitats) (Figure 4.1, 4.2). Reproduction was less successful in ‘closed’ than ‘open’ (Table 4.1); *i.e.*, fewer eggs hatched there, fewer female ticks produced larvae there and those that did produced fewer.

Survival of engorged female ticks

None of the engorged female ticks placed in water in the sedge bog habitat survived to lay eggs (Table 4.1), but they did survive 37 ± 8 d (range 26 - 45d). The number of female ticks that survived and laid eggs differed among the seven other habitat types ($X^2 = 19.14$, df =6, $P = 0.004$) (Table 4.1).

Oviposition

Egg laying by female ticks started earlier in the ‘open’ habitats than in the ‘closed’ habitats. Mean dates of oviposition (date half the number of female ticks in a habitat oviposited) were later in ‘closed’ habitats (Table 4.1). Mean preoviposition period of female ticks differed among the habitat types ($H = 67.12$, df = 6, $P < 0.001$). It was longer in spruce forest than in all other habitats ($P < 0.008$) and longer in willow bog than the other habitats ($P < 0.008$) except spruce forest. Preoviposition period was shorter

Table 4.1 Reproductive parameters of engorged female (EF) *D. albipictus* under field conditions in 'closed' (closed aspen,labrador tea, spruce forest, willow bog) and 'open'(open aspen, grassland, shrubland) habitats in Elk Island National Park, Alberta, 1992.

	'Closed' Habitats			
Parameters	Closed aspen	Labrador tea	Spruce forest	Willow bog
No. of EF	23	23	23	23
No. (%) of EF survived[1]	20 (87)	16 (70)	14 (61)	8 (35)
Mean date of ovip.[2]	May 31	June 2	July 1	June 23
Preoviposition period	38 ± 11	38 ± 5	74 ± 16	57 ± 4
Oviposition period	47 ± 19	42 ± 18	30 ± 15	49 ± 24
No. of eggs per EF	2843 ± 2222	2614 ± 2221	1543 ± 1817	2083 ± 2331
Lifespan of EF	85 ± 16	81 ± 18	105 ± 14	95 ± 18
Incubation period	59 ± 41	54 ± 37	13 ± 27	32 ± 34
Mean date of eclosion[3]	August 28	August 24	August 28	August 26
No. (%) of successful EF	14 (70)	11 (67)	3 (21)	4 (50)
No. of larvae per EF	651 ± 136	343 ± 623	10 ± 14	26 ± 50
Percent eclosion	20 ± 32	12 ± 19	0.5 ± 0.8	1 ± 1

[1] Female ticks that survived and lay eggs

[2] Mean date half the female ticks in that habitat began to oviposit.

[3] Mean date half the batches of eggs in that habitat began to eclode.

Table 4.1 (cont.).

		'Open'	Habitats	
Parameters	Open aspen	Grassland	Shrubland	Sedge bog
No. of EF	23	23	23	23
No. (%) of EF survived	14 (61)	12 (52)	19 (83)	0 (0)
Mean date of ovip.	May 27	May 27	May 22	-
Preoviposition period	34 ± 7	32 ± 13	28 ± 3	-
Oviposition period	47 ± 32	31 ± 23	45 ± 18	-
No. of eggs per EF	2149 ± 1761	2323 ± 2193	2700 ± 2315	-
Lifespan of EF	75 ± 17	69 ± 20	74 ± 17	-
Incubation period	66 ± 34	71 ± 33	77 ± 19	-
Mean date of eclosion	August 16	August 24	August 14	-
No. (%) of successful EF	11 (79)	12 (100)	18 (95)	-
No. of larvae per EF	967 ± 1160	477 ± 870	1649 ± 1962	-
Percent eclosion	34 ± 33	21 ± 29	42 ± 32	-

in shrubland than in closed aspen ($X^2 = 13.83$, df = 1, $P < 0.001$), open aspen ($X^2 = 8.01$, df = 1, $P = 0.005$), grassland ($X^2 = 14.85$, df = 1, $P < 0.001$) and labrador tea ($X^2 = 23.00$, df = 1, $P < 0.001$) and did not differ between other pairs of habitat types ($P > 0.001$). Preoviposition was generally longer in the 'closed' habitats than the 'open' ones (Table 4.2).

Oviposition period, the period of egg laying, did not differ among habitat types ($H = 8.01$, df = 6, $P = 0.237$) (Table 4.1).

Lifespan of oviposited female ticks

Lifespan of engorged female ticks differed among the seven habitat types ($H = 33.03$, df = 6, $P < 0.001$) (Table 4.1). The longest and shortest lifespan were recorded in spruce forest (105.3 ± 13.6) and grassland (68.8 ± 20.4) respectively, (Table 4.1). Female ticks lived significantly longer in spruce forest than in all habitats ($P < 0.008$) except willow bog ($P > 0.008$). Female ticks also lived longer in willow bog than in grassland ($X^2 = 6.98$, $P = 0.008$). Mean lifespan of female ticks did not differ between other pairs of habitat types ($P > 0.008$). Overall, oviposited female ticks lived longer in 'closed' than in 'open' habitats (Table 4.2).

Number of eggs produced by female ticks

Few to many eggs were laid by individual female ticks in the different habitat types but the average number of eggs per female tick did not differ among habitat types ($H = 4.51$, df = 6, $P = 0.609$) (Table 4.1).

Table 4.2 Comparison of D. albipictus reproductive parameters (mean ± 1 Std) Between'closed' and 'open' habitats in Elk Island National Park, Alberta, 1992.

Parameter	'Closed' habitats	'Open' habitats	X^2	P
Preoviposition period	49.4 ± 18.8	31.4 ± 6.9	31.77	< 0.001
Oviposition period	41.8 ± 19.5	42.7 ± 23.8	0.05	0.819
No. of eggs per EF	2387.7 ± 2134.6	2479.7 ± 2081.9	0.23	0.628
Lifespan of EF	90.4 ± 18.6	72.4 ± 17.5	20.18	< 0.001
Incubation period	75.2 ± 16.3	82.3 ± 7.0	3.22	0.073
No. of larvae per EF	408.0 ± 992.9	1123.2 ± 1561.0	11.50	0.001
Percent eclosion	13.0 ± 24.7	33.4 ± 31.9	12.35	< 0.001

Incubation period

Duration of incubation was quite variable between batches of eggs within habitat types and mean incubation period of eggs differed among habitat types (H = 22.86, df = 6, P = 0.001). Though eggs in the 'open' habitats took longer to hatch than those in the "closed" habitats, the difference was not significant (P = 0.073) (Table 4.2). Incubation was longer in shrubland than in spruce forest (X^2 = 7.45, df = 1, P = 0.006) and willow bog (X^2 = 9.48, df = 1, P = 002) and also longer in open aspen than in willow bog (X^2 = 8.34, df = 1, P = 0.004).

Eclosion and longevity of larvae

In general, development was slower in 'closed' habitats than in 'open' habitats. Eclosion began later there, the percent engorged female ticks producing ecloded eggs there was less, percent eggs that ecloded was less, number of larvae was less, and mortality of those larvae occurred earlier. The number of larvae per female tick differed among the habitat types (H = 18.51, df = 6, P = 0.005). More larvae hatched in shrubland than in spruce forest (X^2 = 9.74, df = 1, P = 0.002), and willow bog (X^2 = 6.98, df = 1, P = 0.008). Percent eggs that ecloded was different among habitat types (H = 20.01, df = 6, P = 0.003) being higher in shrubland than in spruce forest (X^2 = 6.83, df = 1, P = 0.009) and willow bog (X^2 = 7.42, df = 1, P = 0.006). Percent eggs that ecloded did not differ between other pairs of habitats (P > 0.009).

Tick larvae died earlier in 'closed' than in 'open' habitats (Table 4.3).

Table 4.3. Longevity of D. albipictus larvae in 'closed' (closed aspen, labrador tea, spruce forest, willow bog) and 'open' (open aspen, grassland, shrubland) habitats in Elk Island National Park.

	Sept 13		Oct 12		Nov 16		Nov 30	
Parameters	closed	open	closed	open	closed	open	closed	open
% larvae alive	54.8	61.7	9.7	55.8	0.0	23.3	0.0	6.3
Mean temp.	9.3	8.5	6.5	6.8	3.4	3.3	2.2	3.2
Mean humid.	30	28	42	38	59	60	79	68

Weather

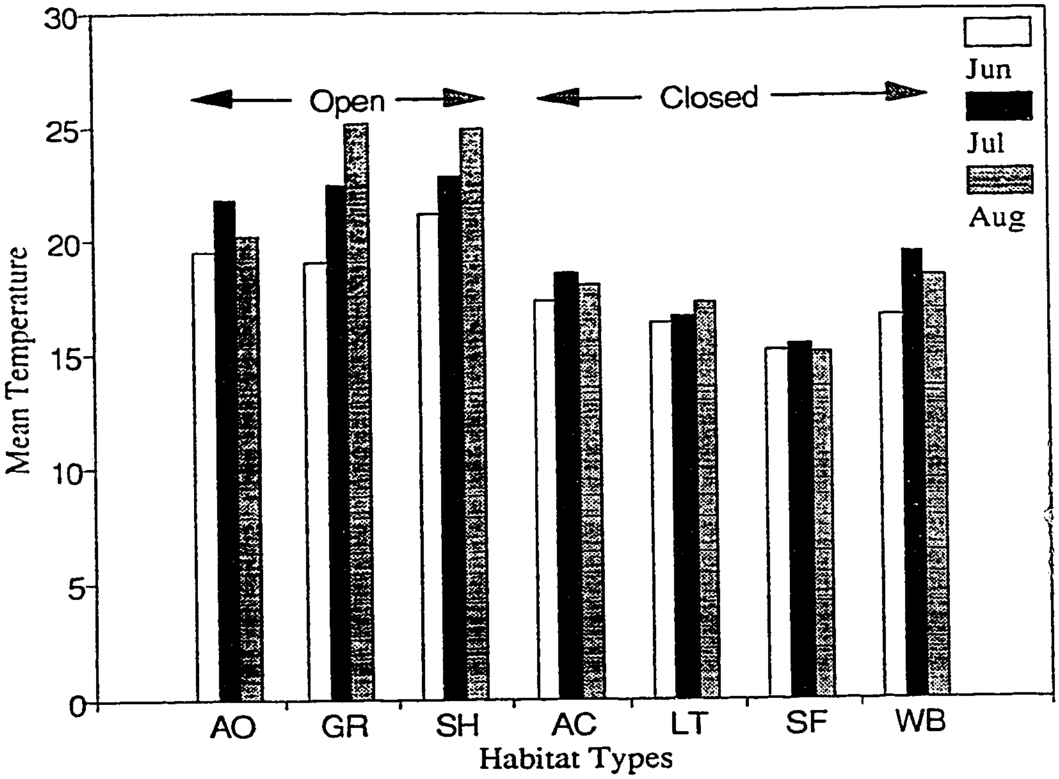
Mean temperatures during oviposition (June), incubation (July), and eclosion (August) were lower in 'closed' than in 'open' habitats (Figure 4.1). Relative humidities were higher. Mean relative humidity was similar between 'closed' and 'open' habitats in June but higher in the 'closed' habitats in July and August (Figure 4.2). Temperature range was wider in 'open' than 'closed' habitats suggesting greater temperature fluctuations in 'open' than 'closed' habitats (Table 4.4).

DISCUSSION

In central Alberta, engorged female Dermacentor albipictus have little option related to selection of oviposition sites in vegetation litter when they drop from moose in March and April, because dispersal is minimal (Drew and Samuel 1986). Where females drop tends to be where they oviposit. If that habitat is suitable, a good crop of tick larvae will be found on vegetation the following autumn. If the habitat is unsuitable, no or few tick larvae will result. In the present study the females placed in habitats with limited canopies (open aspen, grassland and shrubland) *i.e.*, 'open' habitats, tended to be more successful than those that dropped in habitats with more dense canopy (*i.e.*, 'closed' habitats). Barometers of this were the higher percentage of females producing larvae, eggs hatching, and more larvae per female.

Figure 4.1 Mean temperature at experiment sites in eight habitat types in Elk Island National Park in June, July and August, 1992.

Figure 4.2 Mean relative humidity at experiment sites in eight habitat types in Elk Island National Park in June, July and August 1992.


30
25
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Mean Temperature
Open
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Jun
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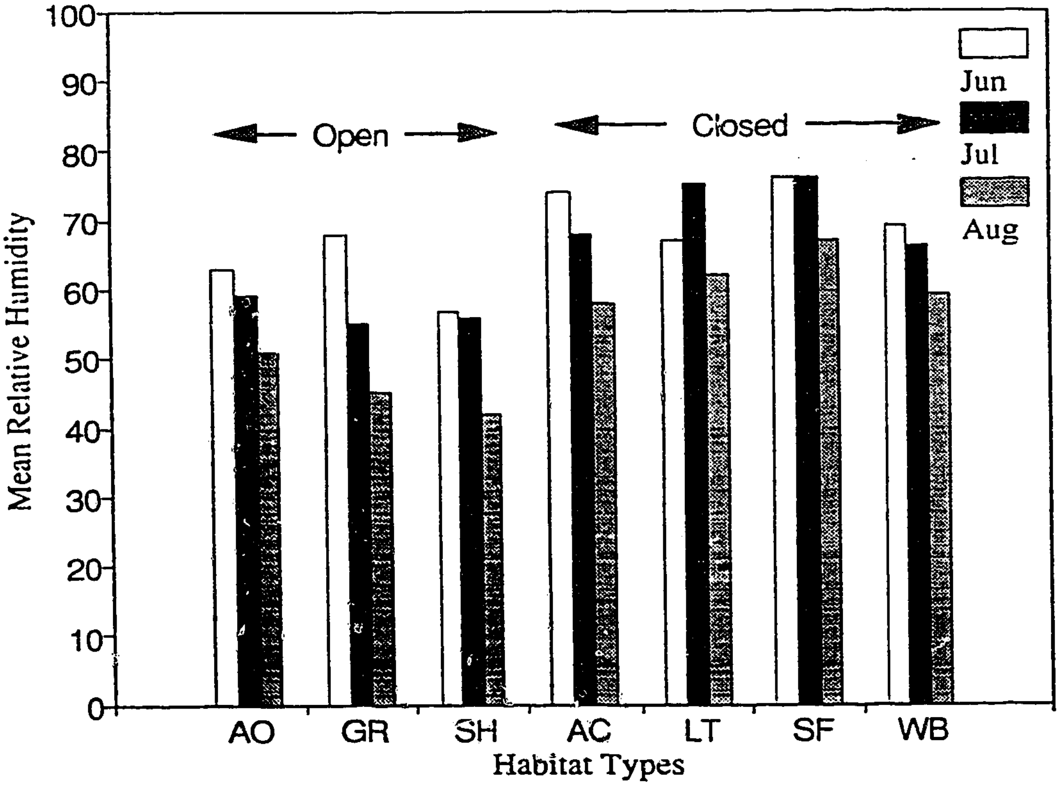
Habitat Types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Mean Relative Humidity
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Jun
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Habitat Types

Table 4.4. Mean temperature and relative humidity (measured between 0900-1300hr) in seven habitat types in Elk Island National Park in June, July and August 1992.

	June		July		August	
Habitat Types	Temp °C (Range)	RH % (Range)	Temp °C (Range)	RH % (Range)	Temp °C (Range)	RH % (Range)
"Closed"						
Closed aspen	17.6(8-26)	73(42-92)	18.5(14-24)	68(53-96)	18.2(8-29)	58(34-80)
Labrador tea	17.5(7-25)	70(48-99)	16.6(15-19)	75(62-90)	15.1(3-22)	65(46-87)
Spruce forest	14.0(8-24)	64(48-99)	16.4(13-18)	72(48-95)	15.6(2-21)	76(51-84)
Willow bog	15.4(8-23)	72(50-99)	19.0(16-24)	66(47-90)	16.0(7-27)	65(46-87)
"Open"						
Open aspen	18.4(8-30)	66(42-88)	21.7(15-26)	59(43-90)	20.2(11-29)	51(30-70)
Shrubland	20.2(9-36)	61(36-90)	22.8(16-31)	56(38-90)	24.7(14-41)	43(20-72)
Grassland	19.0(9-30)	69(38-94)	22.4(15-30)	55(32-95)	25.3(13-38)	45(22-75)

Survival of engorged female ticks

Habitat types in EINP influenced the survival of engorged female winter ticks because of differences in temperature and humidity. Minimum critical threshold temperature (probably 15 °C as suggested by Glines 1983 for laboratory conditions) may be important for female ticks survival in the habitat types because during the female tick dropping season in EINP, ambient temperature never exceeds 25 °C. Saturated moisture conditions were also detrimental to female tick survival.

Drew and Samuel (1986) found that overall survival of engorged female winter ticks in EINP was highest in grassland (37%) followed by bog (34%) and (closed) aspen (13%). However survival of female ticks put out on April 24, 1982 and April 30, 1983 (periods similar to the period of my experiment) were 72% for bog, 44% for aspen and 67% for grassland in 1982 and 64% for bog, 46% for aspen and 77% for grassland in 1983. Female ticks survival in similar habitats in this study were 70% for labrador tea (bog), 87% for closed aspen and 52% for grassland. The differences may be due to: 1) difference in experimental design. Drew and Samuel (1986) used engorged female ticks from captive experimentally-infested moose and the ticks were kept at 10 °C for up to 14 d prior to putting out in the field. Female ticks used in this experiment were collected from a moose carcass (dead 1d) and placed in the habitats within 24 hr; 2) the sites of my experiments were different from those of Drew and Samuel (1986); and 3) variation in weather. Annual changes in weather are common in EINP (Drew 1984) and possibly affect habitat suitability for survival of engorged female ticks. A mild spring, with less temperature fluctuation, can provide optimum temperature conditions in grassland for survival of female ticks, but low temperatures in aspen forest can be unsuitable for survival of female ticks. Minimum threshold temperatures for survival exist for many species of ticks (Sweatman 1967, Drew and Samuel 1986). With changes in weather conditions in the field, habitat suitability for tick survival can change between years. For example, habitats that were suitable for survival of Amblyomma americanum female ticks in a cool year were not suitable the following warm year (Koch 1984).

This is the first report of long-term underwater survival of D. albipictus, although other ticks such Boophilus decoloratus, B. geigyi, and Amblyomma variegatum survived in water for 1 d, 3 d, and 7 d, respectively (Amoo et al. 1985, Dipeolu et al. 1991). Records for this are unknown, but might be related to the near freezing water temperatures in which the ticks were placed.

Physiological, metabolic and developmental processes of most invertebrates (ectothermic organisms) depend on ambient temperature (Block 1990, Beck 1992) and many invertebrates respond to low temperatures by undergoing diapause (Denlinger 1992). The near freezing water temperature in the sedge bog at the time of tick release induced a cold stress on the ticks reducing their metabolic activities. The duration of low temperature condition was probably longer than the period for which female ticks can reverse from cold-induced quiescent state to normal metabolic activity. Also, the period of submergence of the female ticks in water was probably too long for normal physiological and metabolic activities in an oxygen deficient environment.

Results of this study therefore suggest that female D. albipictus cannot survive prolonged water-logging and also long cold temperatures (Drew and Samuel 1986).

Because sedge bog in EINP experiences long period of continuous flooding from snowmelt and summer rains, it is not a suitable tick habitat. This corroborates the low abundance and density of tick larvae in sedge bog during autumn of 1991 and 1992 (chapter 2).

Oviposition

Many investigators (Sweatman 1967, Patrick and Hair 1975, Koch 1984, Fujimoto 1992, Diaz et al. 1991, Despins 1992) have indicated, both in the laboratory and field, that temperature has an influence on the preoviposition period of female ticks, being shorter at high and longer at low temperatures. However, various optimum ranges of temperature (20 - 30 °C) and relative humidity (70 - 80%) exist for oviposition of different species of ticks below and above which pre-oviposition period may increase as a result of retarded egg development. Patrick and Hair (1975), Koch (1984), and Garris et al. (1990) have reported, as I have, shorter pre-oviposition periods in open habitats with high temperatures than in closed habitats with low temperatures. The high temperatures in the 'open' habitats (open aspen, grassland, and shrubland) of EINP likely accelerated tick development including vitellogenesis. Successful oviposition by female ticks in all habitat types with late spring - early summer temperatures varying between 15 and 20 °C and relative humidities between 61 and 73% suggests wide temperature and relative humidity ranges for winter tick oviposition in central Alberta.

Because it is difficult to monitor oviposition by ticks in the field, little is known of the rate of oviposition for many species of ticks (Garris et al. 1990). Possible cues that might trigger oviposition include temperature, relative humidity and photoperiod. Little is known of the effect of photoperiod on oviposition in the field (discussed by Drew and Samuel 1986) though in the laboratory it influences the timing and rate of oviposition (Wright 1969). The similarity in duration of egg laying among habitats suggests that similar biological or environmental cues are acting with similar degree of influence in the different habitat types. One possibility is the heritability of the trait for oviposition period by a tick species under prevailing climatic conditions. Another possible explanation deals with the accumulation of temperature (degree-days) during the pre-oviposition period. There may be a critical minimum threshold of degree-days needed to trigger egg development and once that is reached, temperature will have little influence on rate of egg production (Drew and Samuel 1986).

Lifespan of oviposited female ticks

All engorged female winter ticks were given similar treatment in all the habitat types during the experimental period. While variability in lifespan of individual female ticks within a habitat type may be related to the state of engorgement and physiology of the individual ticks, differences in mean lifespan of female ticks among habitat types were attributed to the influence of the habitat types in which they were released. Different habitat types establish different microclimatic conditions. Drew (1984) observed that temperature and relative humidity differ among habitat types in EINP. Differences in temperature and relative humidity among habitat types during July and August 1992 were also observed during this study (Table 4.3, Figures 4.1 and 4.2).

The longer lifespan of female ticks in 'closed' habitats (closed aspen, spruce forest, willow bog) was attributed to the low temperature and high relative humidity conditions of these habitats which reduced metabolic activities and lengthen development time (Koch 1984). Weather conditions in labrador tea were similar to those in 'closed' habitats (Table 4.3). Low temperatures and high relative humidities in the 'closed' habitats are due to the dense tree canopy that prevents direct incidence of solar radiation. High metabolic activities and fast development, triggered by high temperatures in the 'open' habitats (open aspen, grassland and shrubland) shortened preoviposition period and lifespan of female ticks.

Number of eggs produced by female ticks

Number of eggs produced by female ticks was not different among habitat types suggesting that intrinsic rather than extrinsic factors influence egg production by female winter ticks. Studies on reproduction of many species of ticks show that the number of eggs produced depends solely on the engorged weight of the female tick (Sweatman 1967, Wright 1969, Diehl et al. 1982, Chilton and Bull 1991, Glines 1983, Drew and Samuel 1986, Dipeolu et al. 1991). Because female ticks were randomly selected from the same cohort and released in the different habitat types, mean engorged weight of female tick was probably similar among habitat types.

Incubation period

Temperature is the major factor affecting incubation of eggs of D. albipictus both in the laboratory (Addison and Smith 1981, Glines 1983, Drew and Samuel 1987) and field (Patrick and Hair 1975, Drew and Samuel 1986) because of the influence on rates of physiological and metabolic activities including embryogenesis. In the present study, eggs laid earlier in 'open' habitats incubated longer and hatched synchronously with eggs laid later in 'closed' habitats. This indicates a faster rate of embryogenesis in eggs of later oviposition and a slower rate in eggs of earlier oviposition. Similar results were obtained by Amoo et al. (1985) for eggs of Boophilus decoloratus and B. geigyi and Dipeolu et al. (1991) for eggs of A. variegatum. Balinsky (1965 in Amoo et al. 1985) suggested that the phenomenon may be due to differences in the amount of food reserves between eggs of early and later oviposition, which affect development and viability of the embryo.

Another explanation suggests differential temperature accumulation by eggs in the different habitats during incubation period (Drew and Samuel 1986, Spickett et al. 1990). Eggs laid during lower temperatures accumulate temperature slowly, while eggs laid during periods of high temperature accumulate temperature more rapidly. In EINP, eggs in 'open' habitats were laid earlier, during low temperature regime, and accumulated temperature slowly resulting in slow embryonic development, while eggs laid later in 'closed' habitats, during period of high temperature, accumulated temperature faster resulting in rapid embryonic development. Both groups of eggs may reach the minimum threshold degree-day accumulations required for eclosion at the same time and, thus, hatch synchronously. Temperature degree-day accumulations may be the cause for the differences in incubation period found among habitat types in this study, but as suggested by Drew and Samuel (1986), further study is required. Similar results were reported by Spickett et al. 1990 on eggs of B. decoloratus in South Africa. Other workers (Patrick and Hair 1975, Koch 1984) have also reported the correlation between length of egg incubation and temperature for different species of ticks in the field. Laboratory studies have also shown the correlation between incubation period and temperature for many ixodid ticks (Despins 1992).

The possibility of a diapause by eggs laid earlier during cold periods, as speculated by Drew and Samuel (1986), could result in delayed development and synchrony of eclosion. The synchronous hatching of eggs seems to be a heritable trait in ticks (Dipeolu et al. 1991) and may be important in timing favorable environmental conditions or host availability for transmission. The life cycle of winter tick in EINP is so timed that tick larvae are available during autumn to coincide with favorable weather conditions and active period of moose (principal host) to ensure successful transmission (Drew and Samuel 1986, this study).

Eclosion and longevity of larvae

The number of larvae that hatch from eggs laid by a female tick is the ultimate measure of the reproductive success of that female tick (Chilton 1992). In this study, percent eclosion of larvae was the barometer used to measure the reproductive success of female winter ticks in the different habitat types. 'Open' habitats were more suitable for female tick reproduction in EINP.

The low survival rate of larvae in 'closed' habitats may be due to: 1) long period taken to develop eggs under low temperature conditions, which affect the viability of eggs and, subsequently, longevity of larvae. Amoo et al. (1985) found that eggs of early ovipositions of *B. decoloratus* and *B. geigyi* were more viable and survived longer than eggs of late ovipositions. Eggs of late oviposition contained low protein content and developed into weak larvae with high mortality rate and shorter longevity (Amoo et al. 1985). It is also believed (Dipeolu 1984 in Amoo et al. 1985) that the process of embryogenesis in eggs of late oviposition start in utero and resultant larvae are weak because most of the food reserves that provide energy are depleted during egg development; and 2) low temperature and high relative humidity in the 'closed' habitats, which were detrimental to survival of larvae. Though tick larvae are sensitive to desiccation (Randolph 1993), they do not live long in conditions of high moisture (Yoder and Spielman 1992). Results of this study were contrary to the findings of Garris et al. (1990) who found that a higher proportion of *Boophilus microplus* larvae in Puerto Rico lived in wooded (closed) habitats at any time than in grassland habitats. This is understandable given the very hot climate compared to central Alberta. Temperatures in closed habitats in Puerto Rico may be similar to temperatures in open habitats in central Alberta.

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CHAPTER FIVE

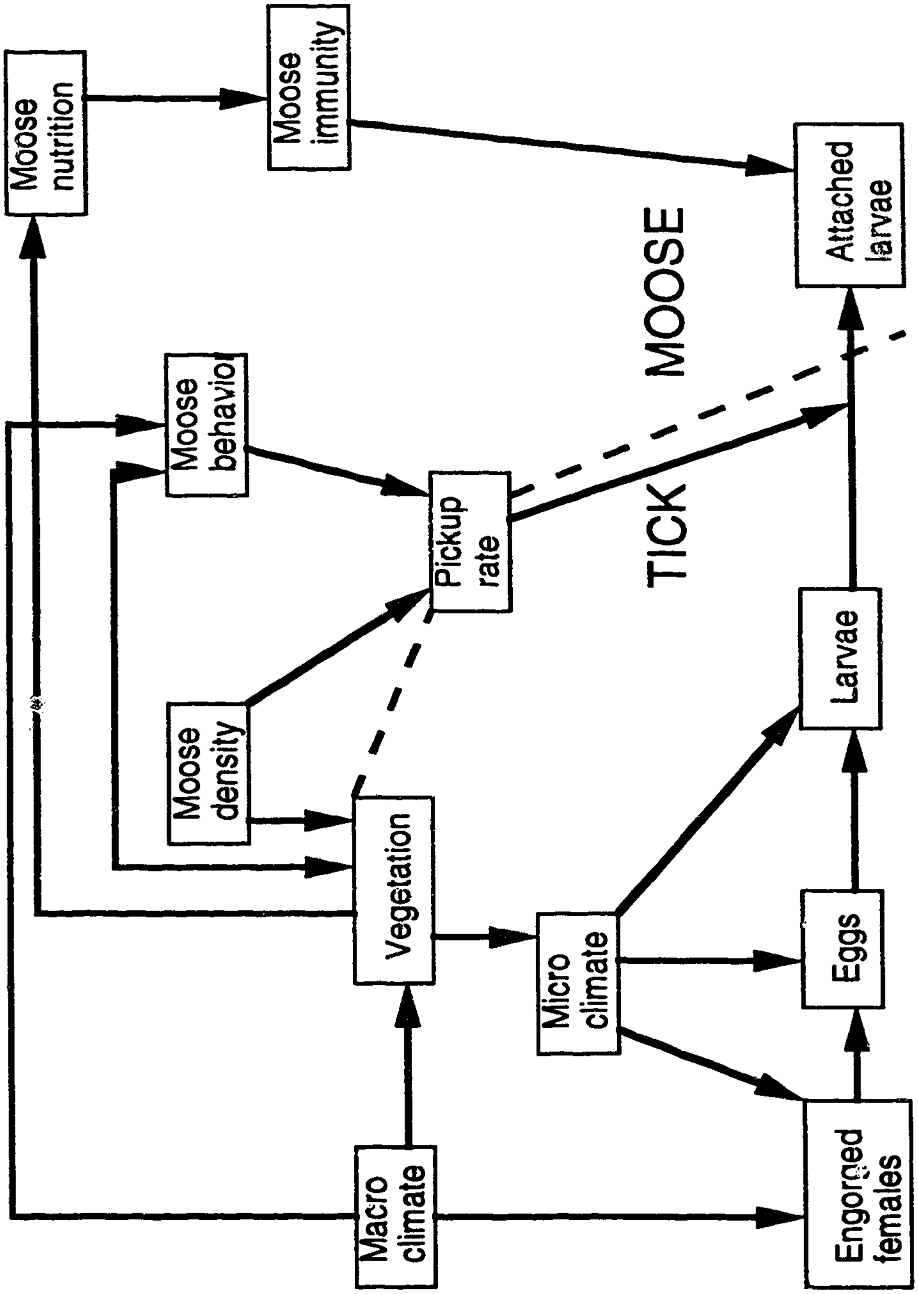
GENERAL DISCUSSION

The life cycle of D. albipictus in central Alberta is one of exact timing between long winters, when ticks are on their main host, moose, and short summers, when ticks are developing off the host in the litter of vegetation. The result is one generation of ticks annually (Drew and Samuel 1989) similar to that as far south as Texas, though the timing in Texas is different (Drummond, pers. comm. 1994). Events critical to transmission of winter tick in EINP include: 1) location (*i.e.*, habitat use) of moose in late March and April, when blood-fed adult female ticks are dropping from moose to the ground to oviposit, and from September to November, when tick larvae are on vegetation seeking a passing vertebrate host, 2) survival of blood-fed, adult, female ticks once on ground, and 3) longevity of tick larvae on vegetation between September to November in various habitats. These events were the focus of the present study. I examined the survival and reproduction of engorged female ticks; distribution, abundance and longevity of tick larvae in eight habitat types; and the influence of biotic and abiotic factors on host-tick contact and transmission of winter ticks in EINP.

Various models of both abiotic and biotic factors have been proposed to elucidate the mechanisms of host-tick contact (Sutherst et al. 1978, Garris et al. 1990, Barnard 1991) or to design control strategies for ticks (Sutherst 1987, 1989). These factors influence the reproductive biology, activity patterns and longevity of ticks as well as the distribution, abundance and behavior of vertebrate hosts. Usually, detailed knowledge of these factors is required to build accurate models. The present study has added more information to the biology of winter tick in the Park. A simple model is proposed here to show the interaction between biotic and abiotic factors that govern the transmission of winter tick to moose in the Park (Figure 5.1). Key components of the model are climate, winter tick, vegetation structure, and moose. Climate affects survival of female ticks in litter during spring, reproduction during summer, and activity patterns and longevity of larvae on vegetation during autumn on one hand, and vegetation structure and productivity and moose behavior on the other hand. The number of female ticks that survive, number of eggs laid, number of eggs that hatch, and longevity of tick larvae are all important in the transmission process. Vegetation structure modifies the microclimate of sites in which ticks drop thus affecting survival and reproduction of female ticks, larvae and moose behavior as stated above. Number, distribution, movement and behavior of moose in the Park during spring and autumn affect the dispersal of engorged female ticks and the pickup rate of tick larvae by moose, respectively. Future research needs to address these factors in detail for a more precise host-tick interaction model.

Though the potential transmission season is from late August - early September to the end of November (Drew and Samuel 1986), the actual transmission period can be much shorter depending on the climatic conditions. For example, in 1991 a snow storm and unseasonable cold weather in mid October shortened the transmission season considerably. However, there is a synchrony of biological processes in EINP that enhance transmission of winter tick larvae. Tick larvae are numerous and very active

Figure 5.1 Diagrammatic representation of some factors affecting transmission of winter ticks to moose in Elk Island National Park, Alberta.


Macro climate
Vegetation
Moose density
Moose behavio
Moose nutrition
Moose immunity
Pickup rate
Micro climate
Engorged females
Eggs
Larvae
Attached larvae
TICK
MOOSE

between mid-September and October at a time when moose are very active in the breeding season (Drew and Samuel 1985). This synchrony in host and parasite activity is possibly an adaptation of winter ticks to enhance transmission to moose during the short window of transmission that occurs in the northern part of the winter tick geographic range. Transmission becomes less efficient as the season progresses because low ambient temperatures and aging of tick larvae reduce longevity of larvae and their ability to quest. At the same time, moose become less active after their breeding season. Seasonality in abundance and activity patterns have also been detected in other species of ticks that appear to coincide with optimum weather conditions or availability of hosts (Schulze et al. 1986, Davidson et al. 1994).

Results of this study indicated that there were no significant differences in distribution and abundance of tick larvae between sites of high and low moose densities. This suggests that some factors other than, or in conjunction with, moose density influenced the distribution and abundance of tick larvae at the sites. These factors might include moose movement, vegetation community structure, terrain and many more. However, moose may largely be responsible for the propagation and maintenance of winter ticks in EINP. Welch et al. (1991) indicated that moose are the major host of winter ticks in EINP and that contributions by other vertebrate hosts to tick population size are negligible. Samuel and Barker (1979) also reported high numbers of winter ticks on moose in EINP. The fact that elk are not suitable hosts of winter ticks (Welch et al. 1991) and were also observed during the field data collection in autumns of 1991 and 1992 to spend most of the day resting in sedge bog, which I found had relatively few tick larvae in autumn, suggest they may contribute little to winter tick populations in EINP.

Defining the distribution and relative suitability of different environments for ticks is necessary to assess the level of risk presented to hosts in each environment (Sutherst 1989). Suitability of an environment is often associated with climate (on broad scale) and weather (on narrow scale) (Semtner and Hair 1973, Koch 1984, see review by Sutherst 1989, Garris et al. 1990). In EINP, environmental suitability for winter tick appears to be associated with temperature and relative humidity defined by vegetation structure (habitat types) as they affect winter tick reproduction and transmission. The different microclimatic conditions among habitat types reflect structural differences which result in some habitats being more suitable for winter ticks than others. Thus, tick larvae, as indicated by tick flagging, were more abundant and higher in density in closed aspen forest, open aspen forest, shrubland and labrador tea than in the other habitat types in EINP. Because closed aspen, open aspen and shrubland with high abundance and density of tick larvae also constitute a greater proportion of EINP they are important for winter tick transmission in the Park. Suitable habitats for winter tick reproduction as indicated by the female tick experiment would be open aspen, shrubland, and grassland. This disparity may be due to low data set from the female ticks study or the number of female ticks that drop in the habitats during spring.

Spruce forest was the least suitable habitat for winter tick reproduction and transmission in EINP. Very few eggs of engorged female ticks released in 1992 in spruce forest hatched and very few larvae were collected by flagging during 1991 and 1992. This is attributed to low temperatures in spruce forest throughout the reproductive and transmission periods of winter tick in the Park (see Figure 4.1). This suggests that minimum critical threshold temperature for winter tick reproduction in the field may be similar to the minimum threshold temperature (15.1 °C) under laboratory conditions reported by Glines (1983) .

In western Canada winter ticks occur as far north as 62° N (Samuel 1989). The northern limit of the geographic distribution of winter tick has been associated with bioclimatic conditions (Wilkinson 1967, Drew and Samuel 1986). With spruce dominating the forests of northern Saskatchewan, Alberta and British Columbia, and southern Yukon and Northwest Territories, and with low survival of ticks in spruce forest (this study), habitat type may play a role in determining the geographic distribution of winter tick.

The assumption that more female ticks dropped in willow bog and sedge bog is based on the fact that they were the most preferred habitats of moose during spring. Willow bog and open-low habitats were also preferred by moose during spring in Minnesota (Berg and Phillips 1974). Peak drop off of engorged female ticks in EINP occurs during spring after snowmelt (Drew and Samuel 1986). Therefore many engorged female ticks drop in these habitats during spring. However, few larval ticks were found in these habitats during autumn 1991 and 1992 (this study). This phenomenon may be one of the factors regulating tick numbers in the Park.

The longer survival of tick larvae in closed aspen, open aspen and shrubland suggests a longer transmission period in these habitats. More tick larvae would be picked up by moose in these habitats in time and space than in other habitats. The low temperatures in closed aspen (pers. observ.) during the transmission season were probably responsible for long longevity of tick larvae. Similar observations were made by Koch for Amblyomma americanum (1984). However, longevity of tick larvae in gauze bags in closed aspen was shorter than in other habitats. Disturbance of tick larvae during observations might have had an effect on larval longevity. But Samantaray et al. (1986) reported that disturbance did not affect the reproductive biology of Hyalomma dromedarii ticks. Also, tick larvae in the gauze bags (hung on twigs) had no option to aggregate on leeward side of vegetation as naturally occurring tick larvae do. Larvae would therefore be exposed to adverse weather conditions that could shorten their lifespan.

MANAGEMENT IMPLICATIONS

Tick-related mortality of moose has occurred at least on five occasions in EINP (Samuel and Barker 1979, Blyth and Hudson 1987) following rapid increase in moose numbers (C.B. Blyth, unpubl. data). To prevent similar occurrences and also improve health and productivity in moose, winter tick population in EINP should be maintained below lethal levels. Success of tick control in preventing disease transmission (see Barnard 1991) or improving livestock production (Pegram et al. 1989) have been reported.

This is the second major study on the ecology of winter ticks in EINP (see Drew and Samuel 1985, 1986, and Drew et al. 1985). These studies have provided important background data on a parasite known to be involved in at least five die-offs which followed rapid increases in moose numbers (C.B. Blyth, unpubl. data). Given the background data on moose numbers and biology of winter tick, it should be possible to better manage winter ticks in EINP and the aspen-dominated vegetation of central Alberta using models similar to those of Sutherst et al. (1978), Garris et al. (1990), and Barnard (1991) developed for cattle ticks and lone star ticks, respectively.

Such models should be based on the assumption that population size of ticks is a reflection of moose density. Thus, use of these models might have more application outside EINP, where numbers of moose can be manipulated more intensely through public hunting. Park policy and public sentiments make direct manipulation of moose numbers in EINP very difficult.

Fire, which might have had historic influences on tick populations, seems to be the only available tool in EINP to manage winter ticks. Fire at critical times, such as in late spring, to kill adult female ticks dropping from moose, and autumn, to kill tick larvae on vegetation, should reduce population size of winter ticks (Drew et al. 1985). Current practice of prescribed burning in EINP in late spring is adequate and should be continued. However, winter ticks should be given much consideration during these routine burns. Prescribed burns should be scheduled at period (first week of May) when the litter is dry enough for a hot fire which would kill female ticks and if the Park can meet its target of burning 1% of the Park (MacDougall, pers. comm. 1994), and probably more, every year, it may be possible to reduce the abundance of winter ticks in the Park. If an autumn burn is to be considered, then it should be done in 2nd-3rd week of October when highest numbers of tick larvae are on vegetation. If the Park target and objectives of prescribed burning are met, open habitats will be created in the Park which are not good habitats for moose and would indirectly reduce moose numbers in the long term. However, the potential risk will be that of creating suitable tick habitats in the Park.

The historic uncontrolled burning of much of Alberta (and other parts of moose range in North America) might be a major reason why there is no mention of tick-related problems for moose in the literature in the 1920's and 1930's. Fire could have regulated tick population size below that resulting in mortality of moose either by direct mortality of ticks or by influencing movements of moose to burned areas where where few ticks survived to reinfest moose. A case in point is that of EINP which started experiencing tick-related problems on moose in the 1930's as a result of restricted burning since the Park was acquired in 1906.

Tick numbers in the Park should be monitored regularly to assess the effect of prescribed burning on tick populations in the Park. This could be done either by collecting tick larvae during autumn in major habitat types or examination of moose for tick in late autumn or in winter.

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APPENDIX

HABITAT SELECTION BY MOOSE (*ALCES ALCES*) DURING SPRING AND AUTUMN IN ELK ISLAND NATIONAL PARK, ALBERTA.

INTRODUCTION

Winter tick (Dermacentor albipictus) an one-host tick, is endemic in Elk Island National Park (EINP), where moose (Alces alces) is the principal host (Samuel and Barker 1979, Blyth and Hudson 1987, Samuel and Welch 1991, Welch et al. 1991). EINP has a mosaic of habitat types which provide food and cover for the five ungulate species; moose, bison (Bison bison), elk (Cervus elaphus), white-tailed deer (Odocoileus virginianus), and mule deer (O. hemionus). Very little is known about the use of these habitats by moose (Cool 1992, unpubl. report). Again, questions on the influence of these habitat types on winter tick distribution, abundance and transmission to moose have been raised. Also, the influence of moose numbers, distribution and habitat use on the proliferation of winter tick in the Park is only a matter of speculation.

Studies throughout North America indicate that moose show seasonal differences in habitat use influenced by vegetational and physiognomic characteristics of the environment (Brassard et al. 1974, Berg and Phillips 1974, Krefting 1974). However, the quantitative and qualitative distribution of food in time and space also has a strong influence on activity pattern and habitat use by ruminants (Cederlund 1989, Cederlund et al. 1989). Seasonal and geographic differences in moose activity patterns are primarily a combination of behavioral and physiological adaptations to forage distribution and seasonal changes in forage quality (Best et al 1974, Nowlin 1974, Risenhoover 1986). Therefore habitat structure is an important factor in the distribution, abundance and activity patterns of animal species including many parasites. It has also been reported that animal habitat use and activity patterns are influenced by harassment from pests (Sutherst et al 1986, Walsh et al. 1992). These factors may contribute to some parts of a habitat being used more intensely by animals than other parts (Barnard 1991).

Almost all studies on habitat selection by animal species lack an evaluation of the presence or suitability of the habitat for parasites and an assessment of the potential of transmission to the animal species. Sympatric distribution of parasites and animal species maximizes the chance of host-parasite contact that enhances transmission and maintenance of some parasitic diseases. Knowledge of daily and seasonal activity patterns of moose is essential to understand the tick-moose contact process in EINP. Habitat use by moose in relation to tick transmission have not been investigated in any of their geographic regions.

OBJECTIVES

The major objective of the study is to determine the patterns of habitat selection by moose and their influence on winter tick transmission in EINP. Specific aim is to assess habitat selection by moose during spring (when engorged female ticks drop from moose) and autumn (when tick larvae on vegetation infest moose).

METHODS

Study area

The vegetation of EINP was categorized into eight habitat types, closed aspen forest (AC), open aspen forest (AO), grassland (GR), labrador tea (LT), spruce forest (SF), shrubland (SH), sedge bog (SB) and willow bog (WB) to which moose observations were assigned. These habitat types are described in detail in chapter 1.

Spring habitat selection

Habitat selection by moose was assessed by direct observations from a helicopter on April 24, 1992. A Bell 206 helicopter flew close transects of about 100 m apart along east-west grids in both the Main Park and Isolation Area of the Park between 0900 hrs and 1400 hrs. Flying height was about 75-100 m above ground and at a speed of about 60 kph. Data recorded during the survey included the time of observation, the sex and age of moose and the habitat type in which the moose was located. The census crew included the pilot, one experienced and two inexperienced observers. The presence of an experienced observer crew member is essential for accuracy of aerial surveys (LeResche and Rausch 1974).

Autumn habitat selection

Moose habitat selection during autumn was evaluated by direct observation of moose between September and November 1992 during the sampling of larvae at the different sampling sites in the Main Park of EINP. Moose sighted while travelling to or from the sampling sites were assigned to the site nearest the observation point. The time of observation, habitat type and activity of moose were recorded. For some of the moose observed sex and age could not be confirmed. Sex and age are therefore eliminated from the data analysis.

The data were analyzed according to Neu et al. (1974) and Marcum and Loftsgaarden (1980). Habitat preference was determined by Chi-square test as outlined by Sokal and Rohf (1981). Habitat preference is taken as the use of a habitat type in a greater proportion than its availability (Walsh et al. 1992)

Data for moose habitat selection in spring were not sufficient for statistical analysis.

RESULTS

Moose selected habitats differently within and between seasons. Habitat selection during spring was linked to food availability while selection in autumn was linked to weather conditions.

Spring habitat selection

A total of 34 moose was located in the different habitats during the aerial survey (open aspen 17, willow bog 8, sedge bog 5, closed aspen 2, shrubland 1, and labrador tea 1). More moose were observed in open aspen habitat followed by willow bog and sedge bog. Closed aspen, shrubland and labrador tea habitat types were [illegible] elected. Moose were not sighted in grassland and spruce forest during the survey.

Autumn habitat selection

A total of 88 moose was sighted in the different habitats from September 16 to November 28, 1992 (closed aspen 59, open aspen 8, grassland 1, spruce forest 2, sedge bog 7, and willow bog 11). No sightings were made in labrador tea and shrubland. Labrador tea habitat type was eliminated for lack of enough data points before the statistical test. Moose did not use the habitat types in proportion to their availability ($X^2 = 49.9$, $\underline{P} = 0.05$) (Table A.1) suggesting preference for some habitat types and avoidance of others. Closed aspen was used significantly more than its availability. Open aspen, shrubland and grassland habitat types were used significantly less than they are available. Willow bog and sedge bog habitats were used in proportion to their availability. Twenty-nine, 6, 41, and 12 moose were sighted at Site 1, 2, 3, and 4 respectively and may reflect the relative abundance of moose at these sites. The number of moose sighted in closed aspen increased from September (7) through October (21) to November (31) with the approach of winter suggesting that preference for closed aspen habitat may be related to weather conditions.

DISCUSSION

By spring, moose like most animals are nutritionally stressed. Malnourished moose therefore select habitats with more food resources to maximize their energy requirements. Because moose use closed habitats for cover during winter (Berg and

Table A.1 Observed and expected values of randomly located points and moose locations by habitat types for autumn 1992 in Elk Island National Park. Alberta.

	Habitat Types																
	AC		AO		GR		LT		SF		SH		SM		WB		
	obs	exp	obs	exp	obs	exp	obs	exp	obs	exp	obs	exp	obs	exp	obs	exp	Total
Points	560	586	442	426	80	77	7	6	25	26	211	200	99	100	132	135	1556
Moose	59	33.1	8	24.1	1	4.3	0	0.4	2	1.4	0	11.3	7	6.7	11	8.7	88
Total	619		450		81		7		27		211		106		143		1644

Phillips 1974), food resources therein will be heavily used and depleted by spring. In EINP, moose may concentrate in closed aspen and spruce forest during the winter. Food resources in open aspen, willow bog, and sedge bog will then not be used much during winter and these habitats would be highly preferred during spring. Preference for open habitats by moose during spring has also been observed in Minnesota, Montana and Wyoming (see review by Berg and Phillips 1974). Berg and Phillips (1974) also reported the selection of willow and open-low habitats by moose during spring in Minnesota. About 60% of their observations were in the willow and low-open habitats. These habitats may be similar to the willow bog and sedge bog habitats in EINP. Nowlin (1974) observed that aspen, aspen-jack pine and aspen-spruce habitat types were highly selected during spring which may be similar to the open aspen and willow habitats in EINP.

Even though moose used the same major habitats during spring as in autumn, the pattern of selection was different. There was a marked switch from open aspen in spring to closed aspen in autumn. Willow bog and sedge bog were selected during both seasons. However, moose used these habitats more in spring than in autumn. Similar change from open habitats in spring to closed habitats in autumn was reported for moose in Minnesota (Berg and Phillips 1974). Krefting (1974) also reported that moose in Minnesota used more open areas in moderate weather and moved into closed areas during severe weather conditions. Pierce and Peek (1984) reported variability in moose habitat selection between seasons in Idaho. Moose used open sites most during summer and least during winter.

Engorged female winter ticks drop off from moose in spring (Drew and Samuel 1986). It is therefore assumed that many engorged female ticks would drop in the open aspen, willow bog and sedge meadow habitat types of EINP during spring. With favorable microclimatic conditions, many tick larvae will be present in these habitats during the autumn. Semtner and Hairs (1973) found that heavy use of habitats by deer was responsible for the high numbers of ticks in those habitats. The open aspen expected to harbor most larvae during autumn was least selected (9.1%) among the preferred habitat types during autumn. The closed aspen which was least selected (5.9%) during spring and should have few engorged female ticks and subsequently, few larvae during the autumn was most preferred (67%) during autumn. Even though willow and sedge habitats were used intensively during spring, they are not suitable habitats for female tick survival and reproduction because very few tick larvae found in these habitats during autumn.

This study shows that moose are using less of their spring habitats during autumn and suggest that they will be picking up less larvae than available in the park. This pattern of habitat selection should enable moose to avoid high infestations by ticks. Periodic change in habitat use by some wild animal species has been reported as an avoidance mechanism to reduce parasite acquisition. The alternate use of groves of yellow-bark acacia trees by yellow baboons (Papio cynocephalus) for sleeping sites reduced the chances of infection by nematode parasites (Hausfater and Meade 1982). Sutherst et al. (1986) reported the avoidance of tick-infested sites by cattle resulting in low infestation.

During epizootic, winter tick infestation on moose exceed 50,000 (Samuel and Barker 1979, Samuel and Welch 1991) and may result in death (Samuel and Barker 1979). Winter tick epizootics have occurred five times in EINP since 1933 (Blyth and Hudson 1987) which suggest that some mechanism must be responsible in regulating the tick population in the Park. The pattern of habitat selection by moose in EINP may be the main mechanism regulating winter tick numbers in the Park. In spring, many engorged female ticks drop in habitats (willow bog, sedge bog) unsuitable for female ticks survival and reproduction and in autumn moose use less of possible heavily tick-infested habitats (e.g., open aspen) consequently avoiding heavy tick infestation. Another regulating factor may be the cold weather during which female ticks drop from moose. Drew and Samuel (1986) reported that only few engorged female ticks that dropped prior to snowmelt (around mid April) survived (11%). The prescribed burning instituted in the park has the potential of reducing tick populations (Drew et al. 1985) but this is infrequent and only few areas are burned on such occasions.

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