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THE UNIVERSITY OF ALBERTA

REPRODUCTION AND TRANSMISSION OF THE WINTER TICK, *DERMACENTOR ALBIPICTUS* (PACKARD) IN CENTRAL ALBERTA

by

MARK LEE DREW

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

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EDMONTON, ALBERTA

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled REPRODUCTION AND TRANSMISSION OF THE WINTER·TICK, *DERMACENTOR ALBIPICTUS* (PACKARD), IN CENTRAL ALBERTA submitted by MARK LEE DREW in partial fulfilment of the requirements for the degree of MASTER OF SCIENCE.

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Date...July 6, 1984.........................

ABSTRACT

The life cycle and reproductive performance of *Dermacentor albipictus* (Packard, 1869) Banks 1907, was studied under field and controlled conditions in the laboratory. Moose (*Alces alces* L.) were used as the definitive host. Several patterns in developmental trends on moose and some aspects of the timing of the reproductive period were predictable and appeared related to environmental variables.

Engorged female ticks dropped from moose from late February to early May. The peak of engorged female drop-off occurred in late March and the weight of engorged females decreased during the drop-off period. Dispersal of dropped engorged females was minimal and survival was dependent on the absence of snow.

Cooler but less variable temperatures and higher relative humidity in an aspen habitat resulted in lower numbers of engorged females that laid viable eggs, a longer incubation period, and a lower percent hatch than found in either a bog or grassland habitat. The onset of oviposition was synchronous in all habitats studied and began in early June. It is suggested that the onset of oviposition under field conditions was dependent on the occurrence of a particular photophase in spring. Hatching did not occur until late August and early September under field conditions.

The transmission period of *D. albipictus* extended from early September to late November. Larvae ascended vegetation in September, reached peak numbers in early October, and declined in numbers until early December.

Movements of *D. albipictus* on moose and subsequent grooming patterns of moose were dependent on instar. Nymphs and adults moved extensively and large aggregations of both stages occurred on the hump and rump of experimentally infested moose. Initial grooming activity by moose was unrelated to tick density or location, but appeared to be directed at a generalized irritation and occurred in areas of easy accessibility.

All laboratory experiments on reproductive performance of engorged females included multiple replicates along a time series. Cold stressing engorged females at various temperatures for one to 42 days resulted in increased productivity and reproductive efficiency and lower larval mortality. Engorged females under fluctuating temperature and relative humidity conditions had a higher mortality rate and lower

reproductive performance than engorged females in either constant, cold stress, or field condition treatment groups. A declining preoviposition period over time, found in all replicates of all experiments, is thought to be due to the photoperiod the engorged females were exposed to prior to collection.

A transmission model showing relative flow rates of *D. albipictus* between ungulate hosts and habitat types in Elk Island National Park, Alberta was constructed. Moose accounted for the majority of the flow of engorged females in spring and received the majority of larvae in autumn. The aspen forest habitat provided nearly all the flow of larvae to hosts in autumn. A predictive equation was derived to estimate infestation levels of moose based on infestation levels the previous spring, date of snowmelt, and summer conditions.

The epizootiology and management implications of infestations of *D. albipictus* on moose are discussed.

ACKNOWLEDGEMENTS

Wisdom is the principal thing, therefore get wisdom.
And with all thy getting, get understanding.
                                        Proverbs 4:7

This study could not have been completed without the help of many people. I would like to convey my appreciation to all members of the Alberta Fish and Wildlife Division, particularly Bill Wishart and Brian Lajeunesse, for help in acquiring orphaned and captured moose calves. I owe a special thanks to all the people that assisted in the raising of moose calves: Michele Anholt, Pat Fargey, Ian Wishart, Dwayne Lepitski, Jayni Caldwell, Deanne Patsula, and Steve Marsden. The "kids" and I will always be grateful. Special thanks are also due to Keith Taylor and Steve Dalimore, Biological Animal Services, for interest and care on maintaining the calves after weaning.

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I. INTRODUCTION

Ticks of the genus *Dermacentor* are common in North America. Some members of the genus can cause serious health problems in man, livestock, and wildlife as vectors of disease and as pests (Gregson, 1956; Arthur, 1960; Burgdorfer, 1970; Balashov, 1972).

Gregson (1956) believes the winter tick, *Dermacentor albipictus* (Packard, 1869), Banks 1907, is one of the most widely distributed ticks in North America. It is the northernmost member of the genus in North America (Wilkinson, 1967), being found to 60° latitude. It ranges over most of southern Canada and the northern United States, and follows the Rocky Mountains south to the Gulf of Mexico in hilly areas (Cooley, 1938; Howell, 1939; Brown and Kohls, 1950). If *D. albipictus* and *D. nigrolineatus* Packard are synonymous, as proposed by Cooley (1938), Bishopp and Trembley (1945) and Ernst and Gladney (1975), the range of this tick potentially covers the whole of North America.

Habitat preferences of this tick are not well defined. Bishopp and Wood (1913) imply a distribution limited to mountainous regions or timbered uplands in western North America, but distribution records at that time were limited. Reports of this tick in eastern North America and in the southwestern United States seem to suggest that the tick can exist in wooded lowlands, aspen parkland, deciduous forests, and shrubby meadows (Hunter and Hooker, 1907; Gregson, 1956). Wilkinson (1967) attempted to show an association between the known distribution of *D. albipictus* in Canada and bioclimatic zones by isopleths of mean annual number of degree days. His conclusions were hampered by a lack of distribution data, but suggest a relationship between the two variables.

The evolutionary history and early distribution of this tick are not known. The Nearctic *Dermacentor* species including *D. albipictus* apparently evolved in North America (Wilkinson, 1967). Anderson and Lankester (1974) feel that *D. albipictus* probably originated on deer and spread to moose.

The winter tick was originally described from a moose (*Alces alces* L.), but has a wide host range. Large cervids including moose, wapiti (*Cervus elaphus* L.), white-tailed deer (*Odocoileus virginianus* Zimmermann), mule deer (*O.hemionus hemionus* (Rafinesque)), black-tailed deer (*O. h. columbianus* (Richardson)), and domestic horses and

1

cattle seem to be the preferred hosts (see reviews of reported hosts in Gregson, 1956; and Arthur, 1960). Other accidental or incidental hosts include beaver (*Castor canadensis* Kuhl) and orn sheep (*Ovis canadensis* Shaw), mountain goats (*Oreamnos americana* (deBlain ile)), bison (*Bison bison* L.), pronghorn (*Antilocapra americana* (Ord)), black bear (*Ursus americana* Pallus), caribou (*Rangifer tarandus* L.), coyote (*Canis latrans* Say), wolf (*C. lupus* L.), and the white-footed mouse (*Peromyscus maniculatus* (Wagner)) (see reviews of reported hosts in Bishopp and Wood, 1913; Gregson, 1956; and Samuel and Barker, 1979).

D. albipictus is the only member of the genus in North America that exhibits a one-host life cycle (Fig. 1). After initial infestation by the larvae, all successive instars develop on the same host individual. Infestation occurs in autumn and the engorged females are usually no longer present on the host by late May.

The life cycle has been studied many times in the laboratory, usually with cattle as the host animal (Bishopp and Wood, 1913; Howell, 1939; Drummond et al. 1969a). Glines (1983) completed the life cycle using captive moose, but did not fully document the instar changes that occur over time. Addison et al. (1979) and Glines (1983) studied the seasonal occurrence of *D. albipictus* on wild moose in Ontario and Alberta, respectively.

The timing of appearance and duration of existence of each instar in the life cycle appear to vary considerably depending on geographical location (Bishopp and Wood, 1913; Howell, 1939; Cowan, 1946; Patrick and Hair, 1975; Addison et al. 1979; Samuel and Barker, 1979; Glines, 1983). The infestation period of the host from larvae to engorged female is considerably shorter in the southern part of the range of this tick (Bishopp and Wood, 1913; Howell, 1939; Drummond, 1967; Patrick and Hair, 1975) than in the north (Cowan, 1946; Addison et al. 1979; Samuel and Barker, 1979; Glines, 1983).

For ticks in general, most researchers agree that the optimum range of conditions for tick survival and reproduction is from 20-30°C with at least 75-80% relative humidity (see review in Diehl et al. 1982). Temperatures less than 15°C or greater than 35°C and relative humidities less than 75% seem to restrict or prevent oviposition and egg hatching, as well as reduce survival of all instars tested. Most researchers arriving at these conclusions have conducted experiments using constant temperatures and relative humidities. Use of these conditions allows comparisons of reproductive potential of ticks
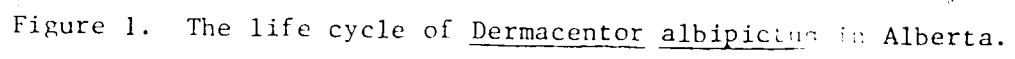
Figure 1. The life cycle of <u>Dermacentor</u> <u>albipictus</u> in Alberta.

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MAR-APR
Engorged females
drop from moose

JUN
Engorged females
lay eggs

JAN-MAY
Adults on moose

JAN-MAR
Nymphs feed
& molt

OCT-NOV
Larvae feed
& molt

OCT-MAR
Nymphs on
moose

SEP-OCT
Larvae ascend
vegetation

AUG-SEP
Eggs hatch
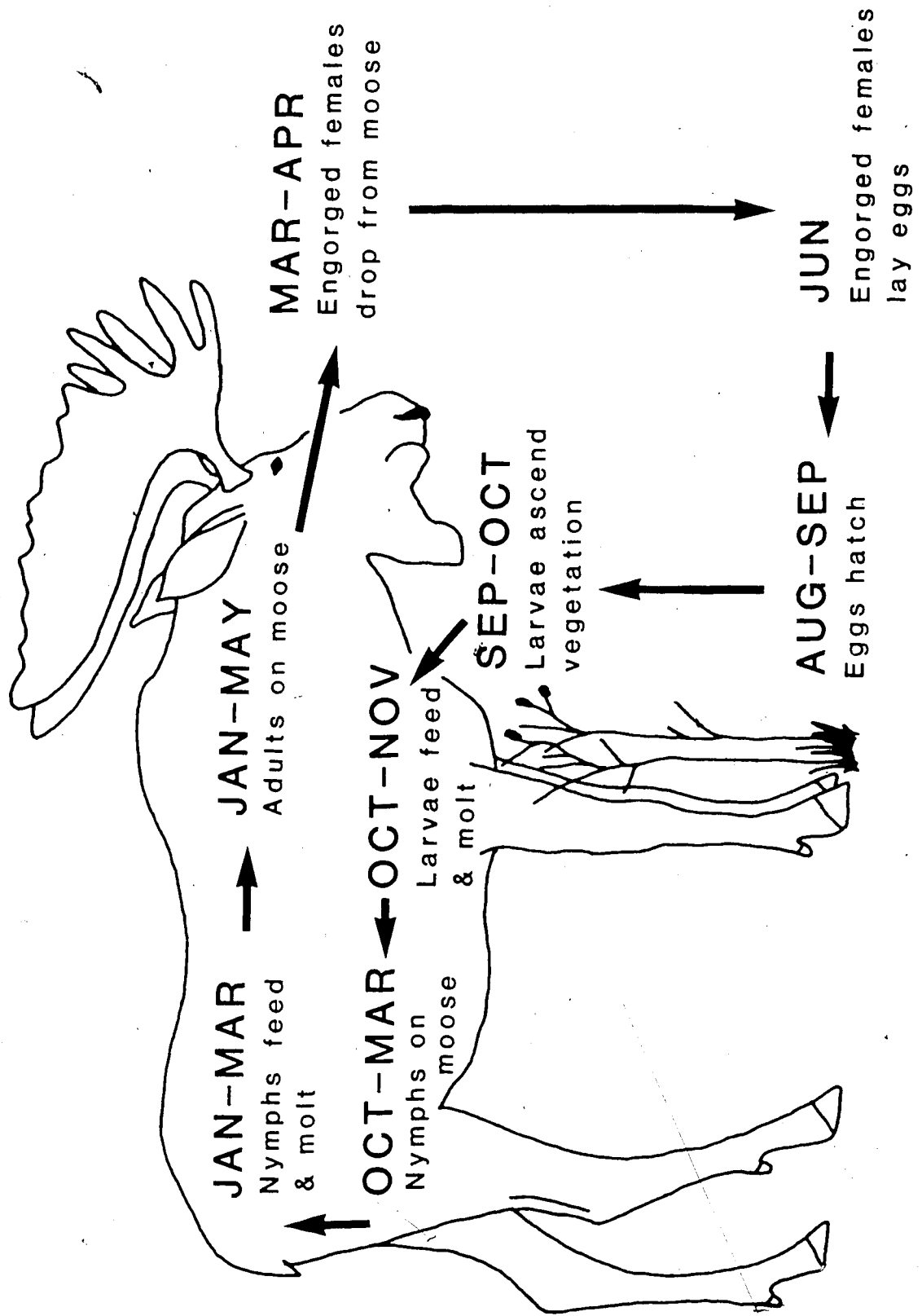
from different parts of the distributional range of a species as well as comparisons between species. Such experiments are also fairly easy to set up and run. However, constant, standardized conditions are rarely encountered under field conditions and this might negate extrapolations of laboratory data to field situations.

Field studies on the reproductive ecology of ticks are uncommon. Temperature and relative humidity appear to be the major influences on reproductive potential and success under field conditions (Hixson, 1940; Hitchcock, 1955; Snowball, 1957; Wilkinson and Wilson, 1959; Harley, 1966), but photoperiod may also be important for synchronizing the timing of the reproductive period with favorable weather conditions (Belozerov, 1982). Most of the published work deals with the cattle fever tick (*Boophilus microplus*) in Australia (Hitchcock, 1955; Snowball, 1957; Wilkinson and Wilson, 1959; Harley, 1966), and the southern United States (Kistner, 1969). Reproduction of *Dermacentor variabilis* and *Amblyomma americanum* was studied under field conditions in Nova Scotia and Georgia (Campbell and Harris, 1979 and Hixson, 1940, respectively).

Observations on the reproduction of *D. albipictus* under field conditions are limited to one major study by Patrick and Hair (1975) in Oklahoma and two observational studies on egg hatching and larval activity in California and British Columbia by Howell (1939) and Wilkinson (1967), respectively. No field work on the reproductive potential of this tick has been done in the northern part of the tick's range where moose are the preferred host.

Winter ticks are regarded as one of the most important parasites and pests of moose (Cowan, 1951; Anderson and Lankester, 1974). Irregular periods of mortality in moose attributed to this tick have been reported since the early 1900's in North America (Cameron and Fulton, 1926-27; Fenstermacher and Jellison, 1933; Hatter, 1950; Cowan, 1951; Ritcey and Edwards, 1958; Webb, 1959; Lynch, 1973; Berg, 1975; Samuel and Barker, 1979; Addison, unpub.). Some of these reports of mortality have occurred when moose densities were high and/or winter weather conditions were severe. Mortality and morbidity of wapiti and mule deer due to infestations of *D. albipictus* have also been reported (Bruce, 1927; Cowan, 1951; Love, 1955; Honess and Winter, 1956).

From 1977 to 1982, many dead and/or debilitated moose were found annually in Elk Island National Park and other areas of central Alberta (Samuel and Barker, 1979;

Samuel and others, pers. observ). Mortality was severe in local areas especially in the winter of 1981-82 (Rippin, pers. comm., and unpub.).

Severe premature loss of winter hair attributed to high numbers of ticks has been documented on moose in Elk Island Park and near Rochester, Alberta (Samuel and Barker, 1979; Glines, 1983). The extent of hair loss on moose in the park is lower than at Rochester, but mortality rates are higher (Samuel and others, pers. observ.; Alberta Fish and Wildlife, unpub). Severe hair loss, anemia, pneumonia, and death have been produced by experimentally infesting moose with *D. albipictus* (Glines, 1983). All are thought to be involved in the recent losses of wild moose in central Alberta (Rippin, unpub.; Samuel and others, pers. observ.).

This study was initiated in an attempt to better understand the epizootiology of tick infestations on moose in central Alberta. A two part study, involving a field and a laboratory component was developed to provide information on the reproductive performance and transmission of *D. albipictus* under field conditions and relate this information to the recent die-off of moose in Alberta. The major objectives were to determine: 1) the distribution and dispersal patterns of engorged females at moose carcass sites in Elk Island National Park, 2) the distribution and dispersal patterns of larvae in autumn in Elk Island National Park, 3) the reproductive potential and timing of the reproductive cycle of engorged females under field conditions and fluctuating conditions in the laboratory, 4) the development, location, and movements of ticks on captive moose over time, and 5) the relationship between tick density, tick location, and grooming activity on captive moose.

II. MATERIALS AND METHODS

A. Definition of terms

The following terms and abbreviations are used extensively throughout this thesis and are defined as follows:

Date out or drop period = date the experimental replicate was begun.

EF = engorged, adult, female *Dermacentor albipictus*.

EF survival = the number of EF that survived and laid eggs.

Experimental replicate = a small number of EF placed in a designated treatment group at predetermined time intervals approximately 2 weeks apart.

Incubation period = time period between the first egg laid and the first egg hatched.

Larval survival = the percentage (%) of larvae that survived until the counting date.

Percent hatch = the percentage (%) of eggs that hatched.

Preoviposition period = time period between initiation of an experimental replicate and the first egg laid.

Reproductive Efficiency Index (REI) = the total production per gram EF (Drummond and Whetstone, 1970), which eliminates the bias of EF weight in reproductive comparisons.

Successful EF = an EF that laid eggs that hatched.

Successful (viable) eggs = eggs that hatched.

Total production = the sum of unhatched eggs, dead larvae, and live larvae on the counting date.

Treatment group = one of 11 different environmental protocols that EF were incubated in for reproductive studies.

Unsuccessful EF = an EF that laid eggs that did not hatch.

Unsuccessful (inviable) eggs = eggs that did not hatch.

B. Description of study area

The major study area for the field portion of this project was Elk Island National Park (EINP) located approximately 40 km east of Edmonton in central Alberta. EINP was established in 1906 through the cooperative efforts of five local citizens and the Federal government for the protection of a remnant wapiti population. In 1930 the area acquired national park status (Parks Canada, 1976).

Currently the park encompasses about 195 km² and is divided into two units. A 136 km² unit located north of Highway 16, is open to the public year around and a 49 km² unit, located south of Highway 16, is used primarily as a restricted access enclosure for wood bison (*Bison bison athabascae* Rhoads). The entire park is surrounded by a 2 m game fence.

EINP lies in the belt of humid continental climate. The mean annual temperature is 1.7°C with daily temperatures ranging from -40°C to 33°C. The average frost-free period is 100 days and the average annual snowfall is 130 cm. Average annual precipitation is 46 cm (Alberta Environment, 1979).

Landforms within the park are classified as dead-ice moraine remaining from the Pleistocene. Scattered bogs, ponds, and lakes are interspersed between small hills and ridges to create a landscape unique to central Alberta (Parks Canada, 1976).

Soils in the park are grouped into 2 broad categories: grey wooded and organic. Most of the parent material is glacial till or lacustrine deposits. Fertility is moderate to poor (Crown, 1977).

The dominant vegetation of the park is comprised of aspen (*Populus tremuloides* Michx. and *P. balsamifera* L.) forests interspersed with grasslands and black spruce (*Picea mariana* (Mill.)) lowlands. Because of the recent absence of fires and logging, the primary vegetation type is old-growth aspen with a dense understory of beaked hazelnut (*Corylus cornuta* Marsh.), aspen, and wild rose (*Rosa* spp.) (Polster and Watson, 1979).

There are five species of ungulates in the park: moose, wapiti, bison (*B. b. bison* L. and *B. b. athabascae*), white-tailed deer, and mule deer.

C. Weather data collection

Temperature and relative humidity were recorded continously in three habitat types (bog, aspen forest, and grassland) in EINP from July to December, 1981 and from April to December, 1982 using hygrothermographs in Stevenson screens set at ground level. Data on minimum and maximum temperature, relative humidity, daily precipitation and accumulated snow depth were obtained as completely as possible from the weather station at the EINP Warden Station for January, 1980 to July, 1983.

D. Vegetation sampling for habitat classification

Two methods were used to quantitatively describe the habitat types at all moose carcass sites. Both methods utilized four randomly chosen points in the vicinity of each carcass site.

The canopy stratum was sampled using the point-quarter method (Cottam and Curtis, 1956). All trees larger than 10 cm (4 in) diameter breast high (DBH) were censused. Relative density, relative dominance, relative frequency, and importance value were calculated for each tree species around each carcass site following the methods of Cottam and Curtis (1956). Sample sizes of carcasses in most habitats were low and a subjective assessment of relative density and importance values was used to group carcasses into habitat types.

Shrub and herb strata were quantified using a 1 sq m quadrat placed on the four points of the point-quarter method. Relative density, relative frequency, and importance values were calculated for each species.

Tree, shrub, and herb species were identified, to species where possible, using the keys of Moss (1955), Cormack (1977), and Newcombe (1977). All habitat sampling was conducted in June when most of the plants were in full leaf and/or flower.

E. Dispersal of engorged females from moose carcasses

Carcasses of moose that were found dead or shot in late winter were tick-infested and assumed to be potential "hotspots" for engorged females (EF) in summer and for larvae the following autumn. Seven carcasses in five habitat types were located and marked in April and May, 1981, and one was found and marked in October, 1981. Seven

moose were shot or found and marked in five habitat types from February to April, 1982. The duff around all carcasses was sampled in May, June and August, 1981 to determine the range and extent of EF dispersal. Only four of the seven carcasses in 1982 were sampled twice (May and June), the others were either scavenged or submerged in water prior to the sampling period.

Sampling was done in 30 cm wide transects orientated in the four cardinal directions from each carcass. Soil duff to a depth of 5 cm and vegetation to a height of 1 m were collected from ten plots along each transect (Fig. 2). Plot size varied with distance from the carcass-the first six were 900 sq cm; the next three were 2700 sq cm; the tenth was 4500 sq cm. Samples were labeled, transported to the University of Alberta and stored at 10°C. Each sample was washed through a series of four screens (smallest mesh size approximately 1 mm) to separate ticks from duff material. All ticks recovered were identified to stage, sexed, and counted.

F. Movements and activity of larval ticks

Carcasses sampled for EF in spring, 1981 and 1982, were subsequently sampled in fall 1981 and 1982, to determine the transmission period of larvae. Sampling was conducted from 7 September to 24 December, 1981 and from 16 August to 20 December, 1982. In addition, all carcass sites were sampled two times the following spring to see if any larvae had survived the winter.

Sampling was conducted two ways. Larvae on the tips of the vegetation were sampled using two 0.5 sq m white flannel flags on a wooden pole. One flag was used for the first 0.5 m away from the carcass, the other was used for the second 0.5 m away from the carcass. Larvae on the ground were sampled using six 30 sq cm white flannel squares laid end to end in four directions from the carcass. Each square was put on the ground for approximately 30 sec. Sampling in 1982 was done using only the two flags. All larvae collected were counted in groups of five and aspirated into a small glass vial using a vacuum apparatus in the laboratory.

Twenty m sections of six game trails were flagged in autumn and early winter, 1981 and 1982, to determine the numbers and density of larvae in these areas.
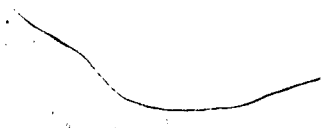
Figure 2. Soil duff sampling pattern around moose carcasses in Elk
Island National Park, Alberta, 1981 – 1982. All
measurements are in cm.
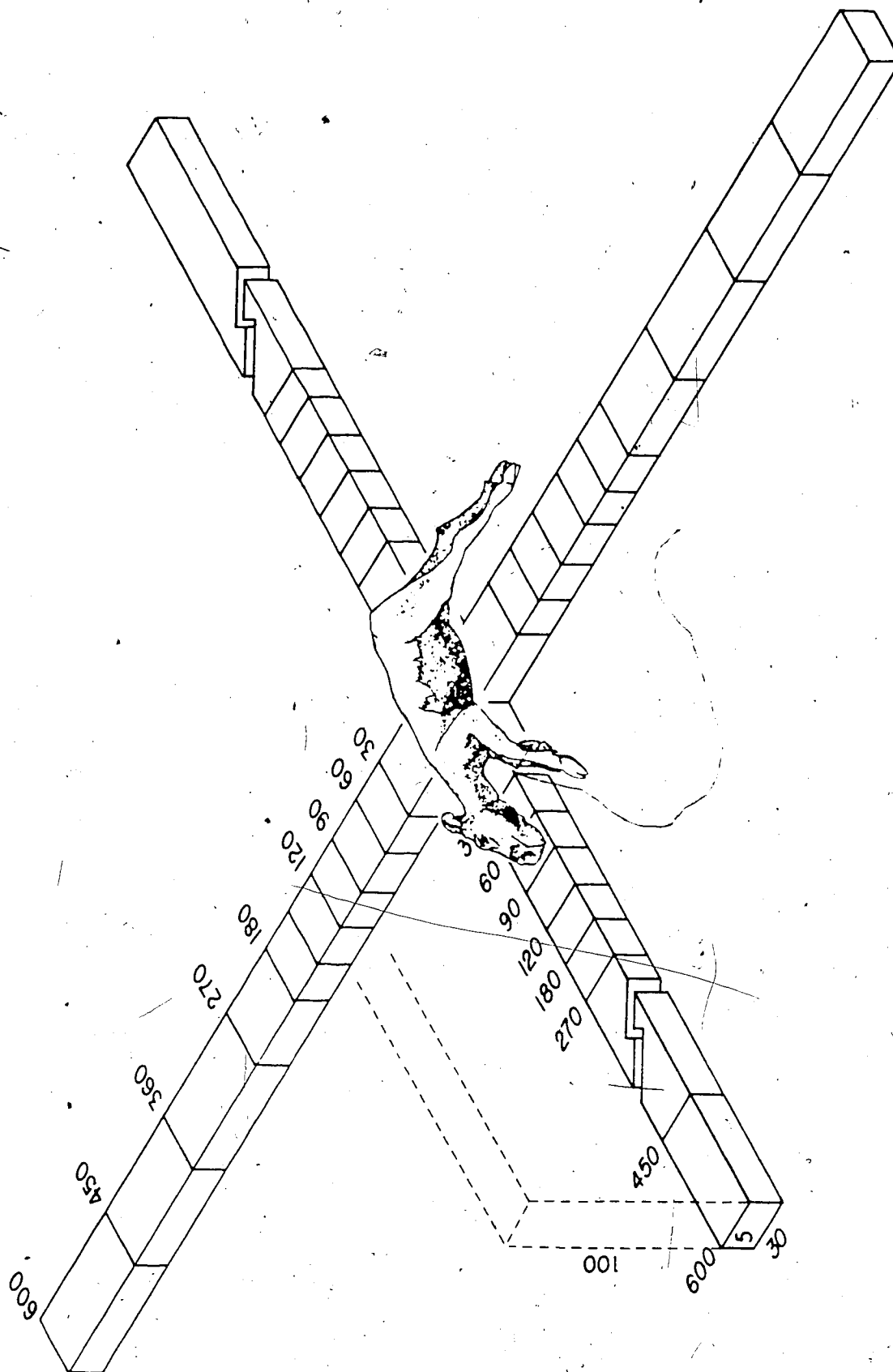
The efficiency of the flagging technique was assessed by seeding three sites in EINP with 5000 laboratory-reared larvae. The larvae were released on 11 October, 1982 and each site was flagged 10 times from 18 October to 20 December, 1982.

Larval *D. albipictus* reared in the laboratory were counted and released onto a series of vegetation plots on the roof of the Biological Sciences Center at the University of Alberta in autumn 1981 and 1982 to observe behavior and activity patterns. Each plot was approximately 1 sq m in area. Larvae were released onto three vegetated plots with progressively taller vegetation (grass, 1-10 cm; aspen shrub, 2-50 cm; aspen shrub, 5-100 cm), and a plot of bare soil with an upright wooden pole 2 m in height to observe climbing and clumping behavior, maximum height of ascension, and reactions to light. All plots were observed every 4-6 hours for the first week after release of larvae and 1-3 times daily thereafter until the experiment was terminated 30-81 days post-release.

Two replicates of four arrangements of four plant species commonly found in EINP: quaking aspen, paper birch (*Betula papyrifera* Marsh), wild rose, and black spruce were used to test vegetation preferences of larvae in 1981 (Fig. 3). Three thousand larvae were released into the center of each of the vegetation arrangements on 13 October, 1981. Larvae on each vegetation sample were counted on 24 November, 1981.

Two replicates of three arrangements of three plant species (beaked hazelnut, quaking aspen, and grass), and a laboratory applicator stick were used in 1982 (Fig. 3). Two thousand larvae were released into the center of each vegetation arrangement on 24 October, 1982. Larvae on each vegetation sample were counted on 25 November, 1982.

The height of larval clumps around carcass sites sampled for larvae in EINP was measured using a meter stick in October, 1981 and 1982. Nine to 38 clumps were arbitrarily selected and measured at each carcass site. Species of vegetation and approximate size of each clump were recorded. Vegetation of the same species without ticks was measured as a control value. All measurements were taken within 6 m of a carcass site.

Figure 3. Arrangement of vegetation in plots for vegetation choice

experiments with larval <u>Dermacentor</u> <u>albipictus</u>. The

release site for larvae was 2 cm from the vegetation samples.

1981

R ●(A/B) S	B ●(R/S) A	S ●(B/A) R	A ●(S/R) B
R ●(A/B) S	B ●(R/S) A	S ●(B/A) R	A ●(S/R) B

●-Larval release site
A-Aspen
B-Birch
R-Rose
S-Black spruce

1982

H ●(A/G) L	A ●(L/H) G	H ●(G/A) L
G ●(H/L) A	H ●(A/G) L	A ●(L/H) G

●-Larval release site
A-Aspen
G-Grass
H-Beaked hazelnut
L-Laboratory applicator stick

G. Experimental infestations of captive moose

Experimental infestations of moose took place at the University of Alberta Biomedical Animal Center located near Ellerslie, approximately 6 km south of Edmonton. The General Purpose Barn on the farm is designed to house large cervids for experimental research.

Young moose calves were captured or obtained as orphans and hand-reared at the Center (see Appendix 1). Four and five calves were weaned in 1981 and 1982, respectively. All animals were housed outdoors in individual pens with concrete floors. They were fed an alfalfa base, pelleted ration supplemented with hay. Food consumption was measured daily. All animals were weighed weekly throughout the experiment.

To determine the appearance and duration of instars of *D. albipictus* in response to exposure period, eight moose calves were infested using two techniques. Three calves (MO 46,50,55) were infested with 30,000 larvae on 15 October, 1981 (mass-infested). The larvae were placed on the moose in six lots of 5000 (Fig. 4). Two moose (MO 60,71) were infested in the same manner on 15 October, 1982. Three calves (MO 59,68,69) were infested with 1000 larvae per day for 30 days from 15 September to 15 October, 1982 (trickle-infested). Larvae were placed on alternate shoulders each day (Fig. 4).

One moose (MO 48) was kept as an uninfested control in 1981 and 1982. Two yearling moose from 1981 (MO 50,55) were reinfested with 30,000 larvae on 15 October, 1982 by mass-infestation.

Larvae for these infestations were from EF collected from moose experimentally infested the previous year. These EF were placed in incubators at 25°C and 85% relative humidity. Larvae were counted using a small vacuum apparatus.

All animals were examined weekly throughout the infestation to determine movements, development, and density of ticks. Each moose was visually divided into eight areas (Fig. 5.). Begining at the spine and ending at the midline, line transects approximately 10 cm apart were searched anterior to posterior by parting the hair. Transects in each of the eight areas were searched on the left side of the animal and all ticks encountered were identified to stage, sexed, and counted. Diagrams of tick location, tick density, and areas of grooming were made for each moose each week.

Figure 4. Infestation sites for moose experimentally infested with

Dermacentor albipictus. Mass-infestation = 30,000 larvae

per moose on either 15 October 1981 or 1982. Trickle-

infestation = 1,000 larvae per day per moose for 30 days

beginning 15 September 1981.

MASS-
INFESTATION

TRICKLE-
INFESTATION
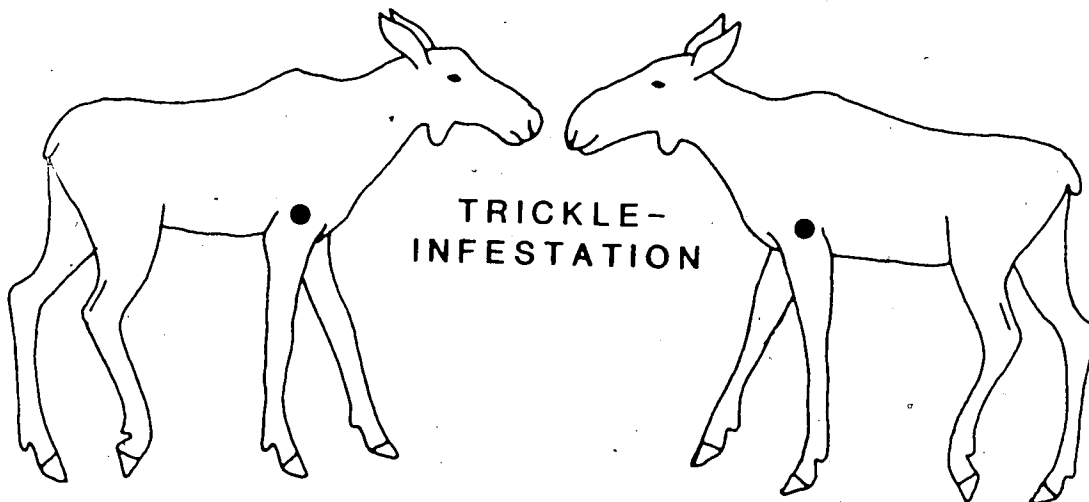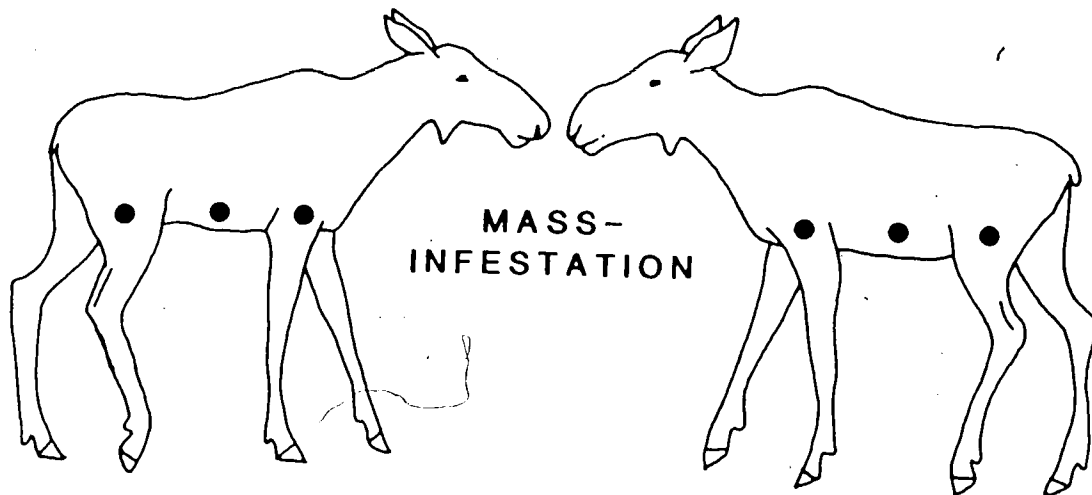
Figure 5. Body divisions of experimental moose for counting and aging ticks and determinations of tick density.
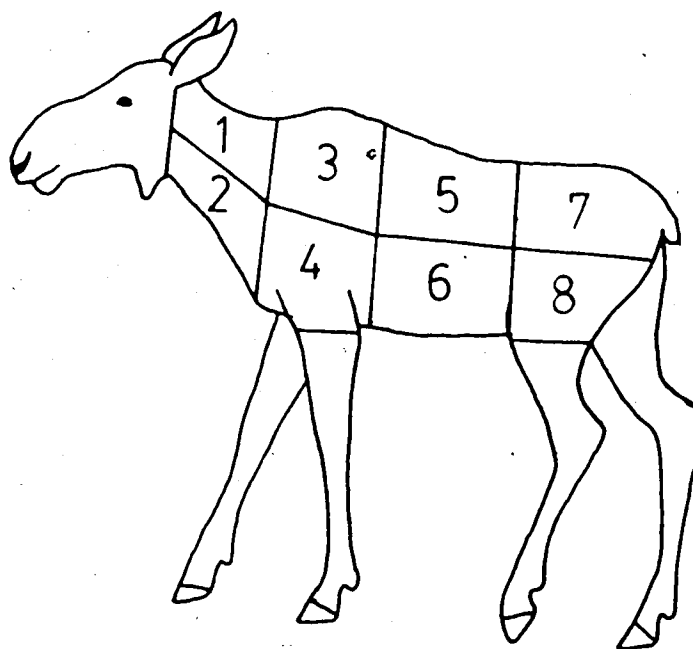
EF were collected from the pens of each moose four times per week from
mid-February to late May in 1982 and 1983. All EF were dried, weighed, and placed in
individual cloth-capped glass vials for use in reproductive experiments.

Production of engorged female ticks

EF were collected as stated above and stored at 10°C in the laboratory for up to
mid c... or until enough had been collected to initiate an experimental replicate (usually
abo 100 EF). An experimental replicate or drop period usually consisted of putting EF
into 11 treatment groups in 1982 and two treatment groups in 1983 (Table 1). EF from
each moose were placed randomly into the treatment groups in both years. The numbers
of EF used in each treatment group varied with time due to the numbers of EF available.
EF were kept in the dark in all laboratory experiments in 1982 and under a 12:12
photophase in 1983. Ticks were monitored two to four times per week for observation
of oviposition and hatching. Unhatched eggs and larvae were counted from 15
September to 18 December 1982, but not counted in 1983.

Reproduction of engorged females under constant conditions

As a control for these reproductive experiments, two to 15 EF, collected as
above, were placed into a 25°C incubator with 85-90% relative humidity each drop period
in 1982. In 1983, six to 18 EF, collected as above, from each experimental moose were
placed in an environmental chamber at constant 19°C with 90% relative humidity and a
12:12 diel photophase each drop period. The EF in this treatment group were monitored
until 1 July, 1983 and only data on EF survival and length of the preoviposition period
were collected. These EF were covered with a cotton cloth to decrease the intensity of
the incident light.

Reproduction of engorged females under field conditions

Eleven screenwire cages were placed in each of three habitat types (bog, aspen
forest, and grassland) in EINP in autumn 1981. These cages were 30 cm in diameter and
40 cm high and were modeled after Semtner et al. (1973).

Table 1.   Conditions used for reproductive experiments with engorged
female <u>Dermacentor</u> <u>albipictus</u>, 1982 and 1983.

Environment	Conditions
Control	constant 25°C for duration, dark constant 19°C for duration, 12:12 photophase
Field	Ambient temperature and light conditions at Elk Island National Park
Cold Stress	−22°C for 2 to 42 days, then held at constant 25°C for duration, dark 0°C for 1 to 34 days, then held at constant 25°C for duration, dark 10°C for 1 to 37 days, then held at constant 25°C for duration, dark ambient temperature at Elk Island National Park for 7 to 42 days, then held at constant 25°C for duration, dark
Fluctuating* Conditions	−5°C 16 hours, 25°C 8 hours for duration, dark 0°C 16 hours, 25°C 8 hours for duration, dark 25°C 16 hours, −5°C 8 hours for duration, dark 25°C 16 hours, 0°C 8 hours for duration, dark 25°C 16 hours, 10°C 8 hours for duration, dark

*Relative humidity fluctuated in anti-phase with temperature, from
40 to 95%.

Three to six EF, in individual vials, from each moose were placed into each of two cages per habitat type every two weeks from early March to mid-May, 1982 and 1983. Two EF from each moose were released free into the same cages each drop period in 1982. No attempt was made to modify the conditions to which the EF were exposed in the cages. If there was snow in the cage, the EF were put on the snow; if not, they were placed in the leaf litter. Ticks were monitored two times per week throughout the summer of 1982, but only until 1 July, 1983, to observe the timing of the reproductive period. Larvae and unhatched eggs were counted from 15 November to 18 December, 1982, but not counted in 1983.

Reproduction of engorged females after cold stress

EF are commonly exposed to varying lengths of sub-optimal conditions for reproduction under field conditions. EF from the three experimental moose in 1982 were exposed to one of four cold stress treatments to determine the effects of this stress period on reproductive timing and potential.

Six to 12 EF collected from each moose as above were placed in a chamber at -22°C each drop period. These EF were retrieved at regular intervals from 2 to 42 days and placed in a constant 25°C, 85-90% relative humidity incubator to allow oviposition and egg hatching to occur.

Six to 13 EF from each moose, collected as above, were placed in a chamber at 10°C each drop period. These EF were retrieved at regular intervals from 1 to 37 days and placed in the 25°C incubator for completion of reproduction.

Five to 14 EF, also collected as above, were placed in a chamber at 0°C each drop period. These EF were retrieved at regular intervals from 1 to 34 days and placed into the 25°C incubator for completion of reproduction.

Five EF from each moose were placed in a 'common' cage in each habitat type in EINP each drop period. These EF were retrieved at regular intervals from 7 to 42 days and placed in the 25°C incubator for observation of reproduction.

Reproduction of engorged females under fluctuating temperature and relative humidity

EF in the field are normally not subjected to the constant conditions of temperature and relative humidity used by most laboratory researchers. To determine the effects of continual fluctuations of temperature and relative humidity on reproductive timing and potential, EF collected from the three captive moose in 1982 were placed in environmental chambers that fluctuated temperature and relative humidity on a predetermined schedule. Three temperature and relative humidity levels, all commonly found during the period of EF drop-off in Alberta, were utilized. Two to four replicates of each treatment were made.

Eight to 26 EF from each moose, collected as above, were placed in a chamber that fluctuated from -5°C for 16 hours to 25°C for 8 hours. The relative humidity fluctuated in anti-phase with the temperature, usually from about 40 to 95%.

. Two to 25 EF from each moose, collected as above, were placed in a chamber that fluctuated from 0°C for 16 hours to 25°C for 8 hours. The relative humidity fluctuated within the same general limits of the previous treatment.

Three to 21 EF from each moose, collected as above, were placed in a chamber that fluctuated from -5°C for 8 hours to 25°C for 16 hours with a corresponding reversal in periods of high and low relative humidity.

Four to 23 EF from each moose, collected as above, were placed in a chamber that fluctuated from 0°C for 8 hours to 25°C for 16 hours with reversed periods of high and low relative humidity.

Eleven to 35 EF from each moose for two drop periods, collected as above, were placed in a chamber that fluctuated from 10°C for 8 hours to 25°C for 16 hours. The relative humidity in this chamber was within the same general range as that in the other fluctuating temperature chambers.

Reproduction of engorged females from other host species

EF from free-ranging moose, white-tailed deer, and wapiti, and from tame wapiti were obtained and incubated at 25°C, 85-90% relative humidity for comparative reproductive studies with EF from experimental moose under the same conditions.

I. Data analysis

All data were analysized using the Michigan Interactive Data Analysis System (MIDAS) (Fox and Guire, 1976). Arcsin transformations of data in percent form (EF survival, percent hatch, and larval survival) were done prior to statistical analysis, but are shown in tables as percent values equivalent to the transformed values. Comparisons of means were done using ANOVA. Specific differences between means were identified using an F-test for linear combinations and a Neuman-Kuehls test. Comparisons of regression lines were done using covariance analyses.

III. RESULTS

A. Weather data

Because one of the major objectives of this study was to describe the reproductive potential of EF *Dermacentor albipictus* under field conditions, weather conditions recorded during these reproductive trials are presented here. Differences in weather between habitat types will be discussed in later sections as part of the expxlanation for differences observed in the reproductive output of EF in the three habitats studied.

Annual trends in temperature, precipitation, and snow accumulation at the EINP Warden Station from 1980-1983 are shown in Appendix 2. Snowfall and rainfall were generally sufficient to maintain adequate soil moisture over the course of this study.

Temperature patterns in the three habitat types in EINP in 1981 and 1982 (Appendix 3) were generally similar to those at the EINP Warden Station (Appendix 2), however, some differences in temperature were observed between habitat types. Although the hygrothermograph in the grassland malfunctioned at irregular intervals in winter, 1981-82 and most of summer, 1982, temperature trends were similar in the bog and grassland (Appendix 3), both of which had open canopies and were exposed to high levels of solar insolation. Although mean maximum and mean minimum temperatures were not significantly different in the three habitats in 1982, maximum and temperatures in the aspen forest, which had a dense canopy, were lower for 16 of 34 weeks (x^2, 2 df = 14.1, $p<0.05$), and higher for 25 of 34 weeks (x^2, 2 df=36.2, $p<0.05$), than in either the bog or grassland (Fig. 6). Mean maximum temperatures in the bog were higher than in the aspen (t, 11 df=2.08, $p<0.05$), and mean minimum temperatures were lower than in both the aspen and grassland (t, 11 df=3.95 and 1.72, both $p<0.05$) during the critical period for EF reproduction (June-September). From June to September, mean maximum temperatures in the aspen were lower in all but one week, and mean minimum temperatures higher in all but three weeks, than in the bog or grassland (x^2, 2 df=20.0, $p<0.05$, x^2, 2 df=26.0, $p<0.05$ for mean maximum and mean minimum temperatures, respectively) (Fig. 6). Summations of hours over 15°C and 20°C also suggest habitat differences in temperature, with the bog having the highest total number of degree hours
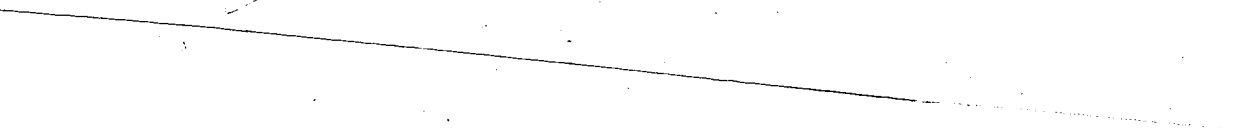
Figure 6. Mean weekly maximum and minimum temperatures for three habitat
types in Elk Island National Park, Alberta, 1982. O - bog,
● - aspen, □ - grassland.
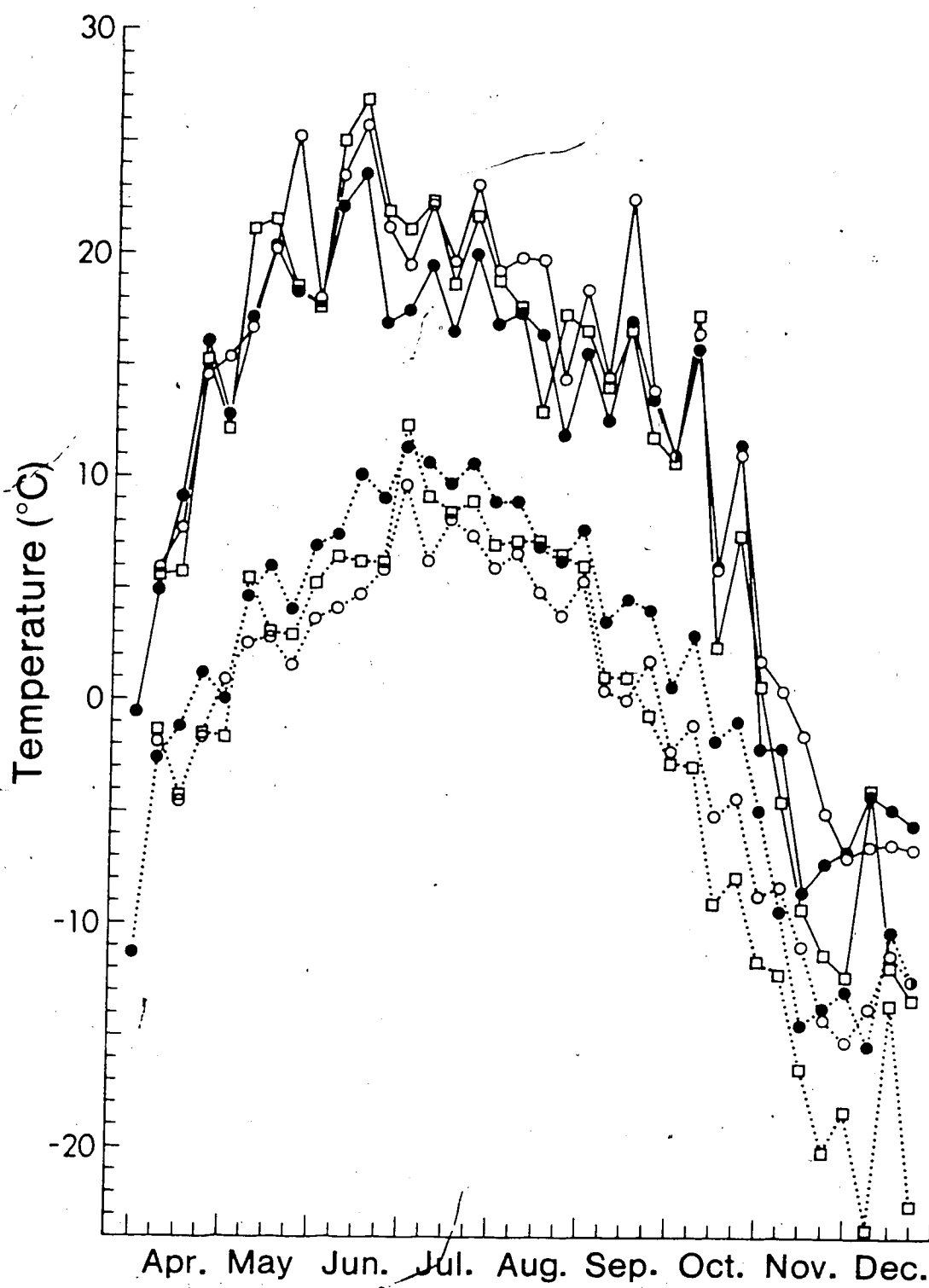
over both 15 and 20°C (Table 2) during the critical period for EF reproduction.

Daily fluctuations in temperature were dampened in the aspen resulting in more stable conditions than in either the bog or grassland (Fig. 7). The greatest fluctuations in temperature and the highest relative humidity were found in the bog, probably due to its physical characteristics as a frost pocket with a high water table.

There was an annual trend in relative humidity ranges in the three habitats from low values in winter to high values in summer (Appendix 3). Despite wide daily fluctuations, relative humidity usually averaged between 70-80% during the spring and summer. The maximum daily relative humidity was usually reached at night with the daily minimum during the hottest period of the day. There was no consistent pattern in the daily variation in relative humidity in the three habitats (Fig. 8).

B. Vegetation sampling for habitat classification

Carcasses were grouped into six habitat types (Appendix 4) using the point quarter and quadrat sampling methods. The relative density, relative dominance, relative frequency, and importance values for each tree species sampled at each carcass site and the relative density, relative frequency, and importance values for each shrub and herb species sampled at each carcass site are tabulated in Appendices 4 and 5, respectively. Importance values may be over-estimated due to small samples sizes in most habitat types.

Three habitat types (bog, aspen, and grassland) were utilized extensively for field work in this study. These habitat types represented the 'extremes' (bog and grassland) and the 'average' (aspen) conditions found in EINP. Scattered spruce and paper birch were the only trees present in the bog, although very few were larger than 10 cm DBH. The shrub/herb layer was dominated by laborador tea (*Ledum groenlandicum* Oeder), cranberry (*Vaccinium* spp.), and sphagnum moss (*Sphagnum* spp.). The duff layer was very sparse and consisted of pockets of old leaves between hummocks of sphagnum.

The aspen forest habitat was characterized by a dense canopy and relatively low densities of trees. The shrub layer was dense, consisting of rose, beaked hazelnut, and quaking aspen. The herb layer was dominated by small shrubs, forbs, and grass. The duff layer was thick, usually 5 to 8 cm.

Table 2. Temperature summations (degree hours) over 15°C and 20°C in three habitat types in Elk Island National Park, Alberta, 1981 and 1982.

| | 1981 | | | | | | 1982 | | | | | |
| | Bog | | Aspen | | Grassland | | Bog | | Aspen | | Grassland[a] | |
Month	15°C	20°C	15°C	20°C	15°C	20°C	15°C	20°C	15°C	20°C	15°C	20°C
Apr	---	---	---	---	---	---	20	0	26	2	16	1
May	---	---	---	---	---	---	169	56	186	70	138	80
Jun	---	---	---	---	---	---	297	176	260	103	259	119
Jul[b]	122	35	159	8	72	17	281	166	222	51	203	97
Aug	382	286	371	174	195	62	191	67	111	7	134	43
Sep	144	80	135	55	106	51	149	53	116	3	87	19
Oct	23	0	6	0	5	0	25	6	19	3	14	1
Nov	2	0	3	0	0	0	0	0	0	0	0	0
TOTAL	673	401	674	237	478	230	1132	524	940	239	851	360
Total 1 Jun-1 Sep	---	---	---	---	---	---	769	409	593	161	596	181

[a] A complete hygrothermograph record was not available for this site.

[b] Hygrothermographs operable after 20 July, 1981.

Figure 7. Variation between mean weekly maximum and minimum temperature
in three habitat types in Elk Island National Park, Alberta,
1981 and 1982. O - bog, ● - aspen, □ - grassland.
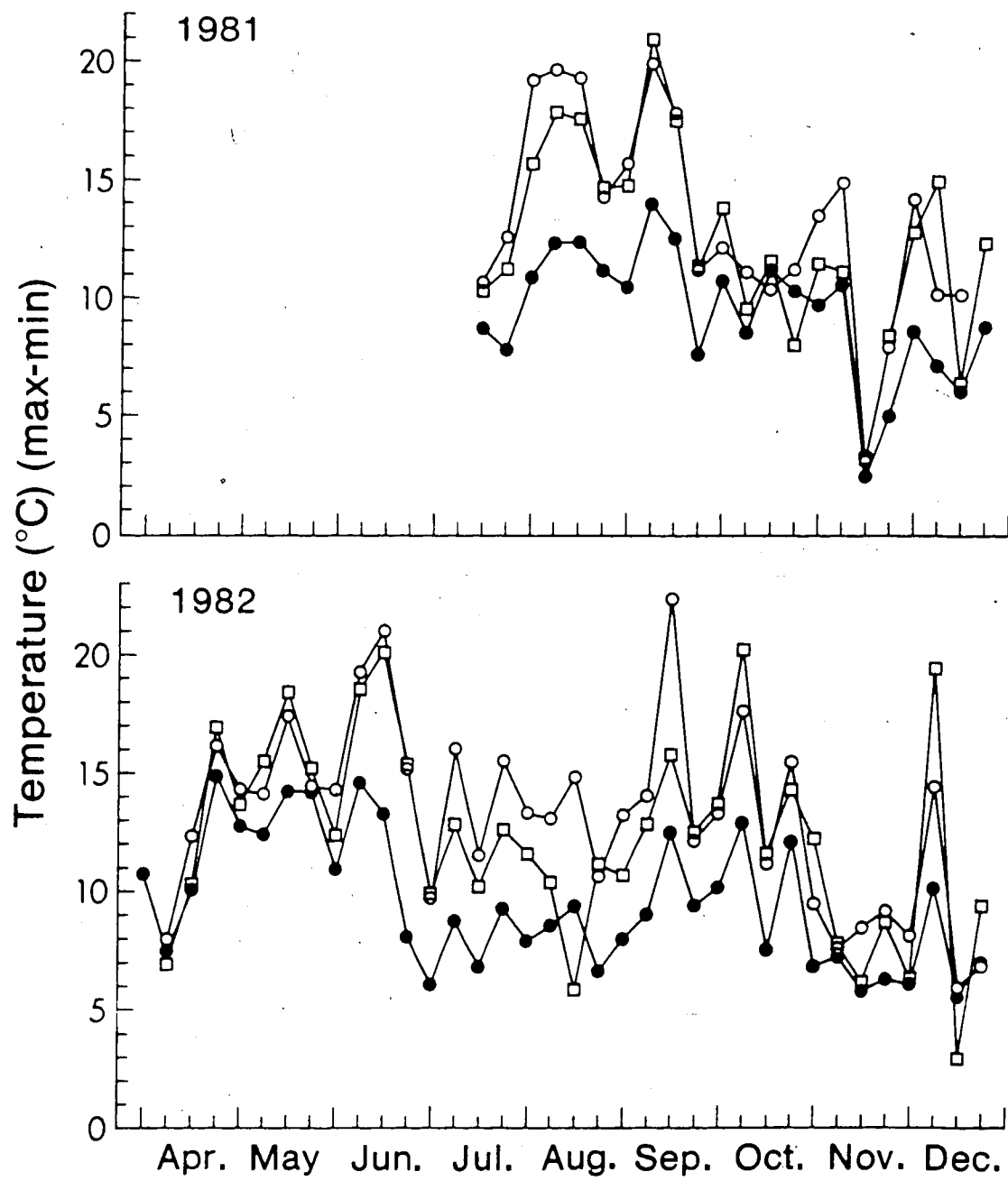
Figure 8. Variation between mean weekly maximum and minimum relative
humidity in three habitat types in Elk Island National Park,
Alberta, 1981 and 1982. O - bog, ● - aspen, ☐ - grassland.
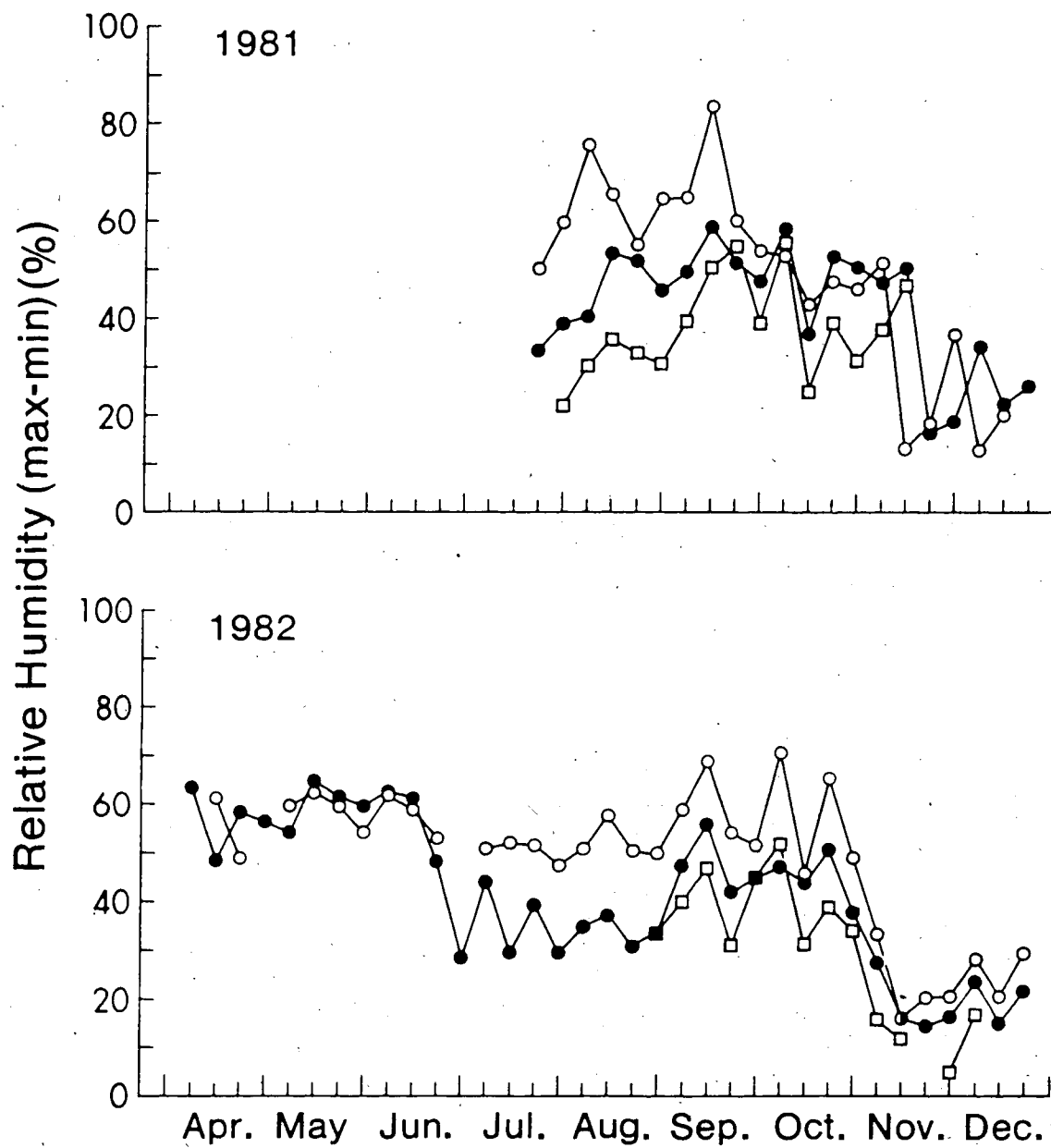
No trees were present in the grassland habitat, but the shrub/herb layer did contain a few rose and aspen. Duff was sparse, usually less than 2 cm, and limited to areas around clumps of grass. Areas of bare soil were common.

C. Dispersal of engorged females from moose carcasses

EF were found in the duff layer at nine of the 11 carcass sites sampled, however, dispersal of EF from carcasses was minimal. Of the 265 EF were recovered in 1981-1982, 56% and 87% were recovered within 30 and 60 cm of the carcass, respectively. Only six EF (2%) were found farther than 180 cm from the carcass.

D. Movements and activity of larval ticks

A total of 2394 larvae was recovered by flagging the three sites seeded with 5000 larvae giving an efficiency for the flagging technique of 16% (14%, 21%, and 14% in the bog, aspen and grassland, respectively). Flagging for larvae around carcasses and along trails was asssumed to be reasonably similar in efficiency. Because only a small proportion of the larvae around the carcass sites were removed by the flagging technique, it was assumed that the results reported here reflect actual changes in larval numbers under field conditions rather than removal due to the sampling technique.

Flagging results indicated that larvae were available for transmission to hosts by early September. In 1981, larvae were recovered from vegetation on 14 September at three carcass sites. No clumps of larvae were seen at these carcass sites the previous week indicating that larvae ascended vegetation between 7 and 14 September, 1981. Sampling in 1982 was started on 27 August but larvae were not recovered until 6 September. Larvae of the free EF in the cages in EINP began to ascend vegetation and the sides of the cages 10-14 days after hatching and began to form clumps by late August and early September.

Larval *D. albipictus* were recovered from vegetation by flagging at all seven carcass sites in 1981 and at one of five carcass sites in 1982 (Fig. 9). They appeared on the tips of the vegetation in early September; numbers rose rapidly, and peaked in early October. By mid-November, larval numbers began to decline rapidly and were at or near zero by late December. Some larvae remained viable on the vegetation until mid-Feburary.

Figure 9. Changes in mean numbers of Dermacentor albipictus larvae
collected by flagging around moose carcasses at Elk Island
National Park, Alberta, 1981 (O) and 1982 (●). Seven
carcasses and one carcass were flagged in 1981 and 1982,
respectively.
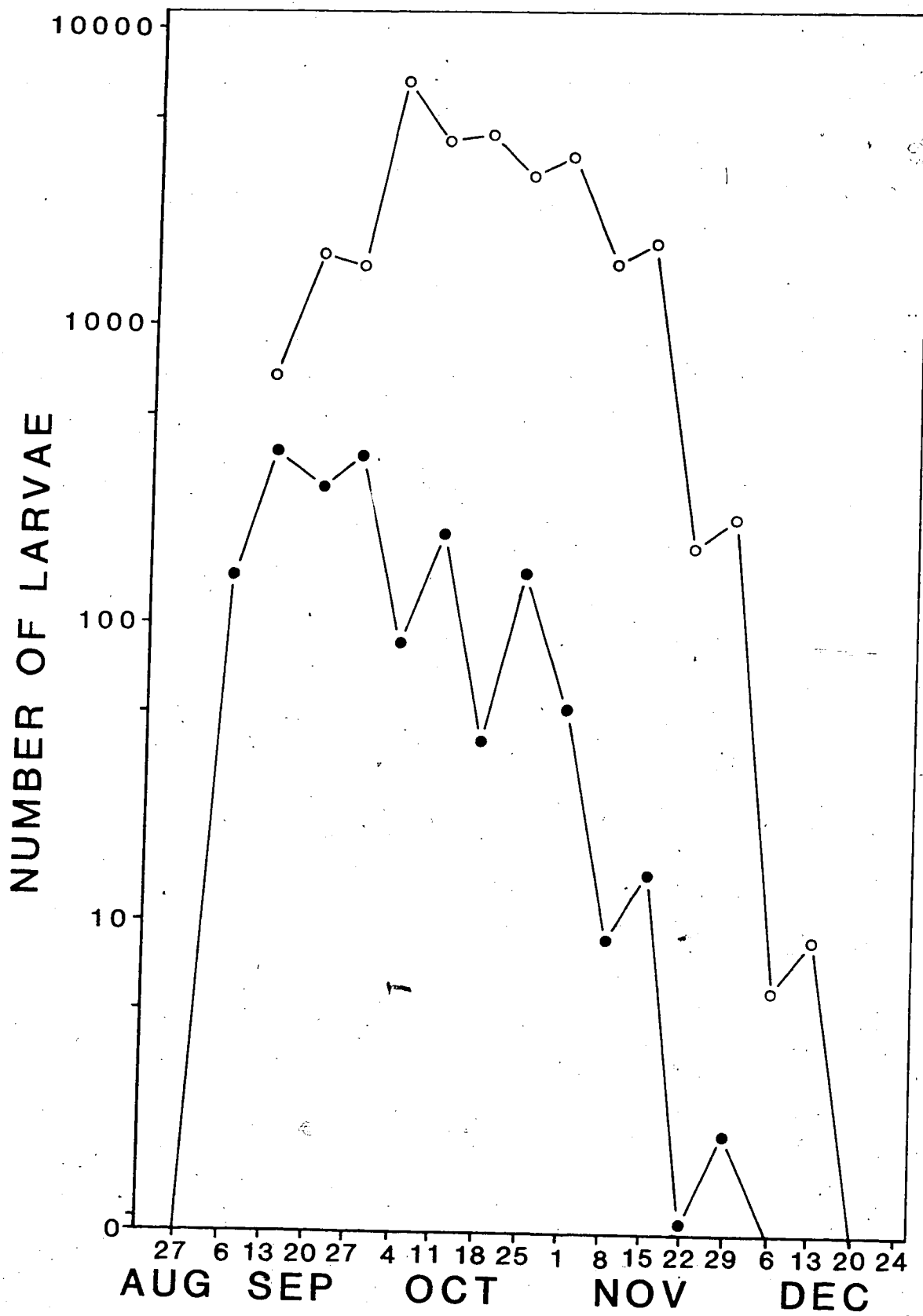
Sampling for larvae on the ground was imprecise due to contamination of the square with larvae from surrounding vegetation while positioning it on the ground. In spite of this problem, the numbers of larvae rose, peaked, and declined in a similar fashion to numbers collected by flagging (Fig. 10).

Numbers of larvae flagged along game trails were lower than at carcasses (Fig. 11), but the general decreasing trend in larval numbers was similar to that at the carcass sites. Only 39 larvae were recovered in the 17 weeks of sampling along game trails in 1982, compared to a total of 2005 flagged in 1981.

Larvae consistently ascended to the maximum height of available vegetation and artificial supports both on the roof of the Biological Sciences Center and in EINP, although no preferred height was observed. Almost all larvae aggregated into clumps on the tips of vegetation (Fig. 12). Clump height varied from 4 cm to 4 m off the ground and was almost always at or near the tips of the vegetation.

Observations of marked clumps of larvae on the roof and in EINP suggested that larvae did not exhibit a diurnal, vertical migration. Clump position remained unchanged in 59 of 65 (92%) observation periods, suggesting that once larvae had ascended, they remained clumped on the tips of the vegetation until they were either picked up by a host, blown off by the wind, or they died.

Few specific conclusions could be drawn on preferences of vegetation species by larvae in EINP because sample sizes of vegetation with and without larval clumps were small in all but the aspen habitat. In the aspen habitat, grass, rose, beaked hazelnut, balsam popular, and quaking aspen were the most frequently occurring species over one m in height (Appendix 5). The mean height of larval clumps was very close to the mean height of the available vegetation (Table 3). Higher numbers of clumps were found on grass, possibly reflecting its importance value in the shrub/herb layer (Appendix 5). The largest clumps were found on aspen in spite of its relatively low importance value, possibly indicating an attraction to or preference for this species of vegetation (Table 3). Results of vegetation-choice experiments with larvae on the roof of the Biological Sciences Center were also inconclusive, suggesting no clear vegetation preference or selection by larval winter ticks (Table 4).

Figure 10. Changes in mean numbers of <u>Dermacentor</u> <u>albipictus</u> larvae

collected by the flannel square technique around seven moose

carcasses at Elk Island National Park, Alberta, 1981.
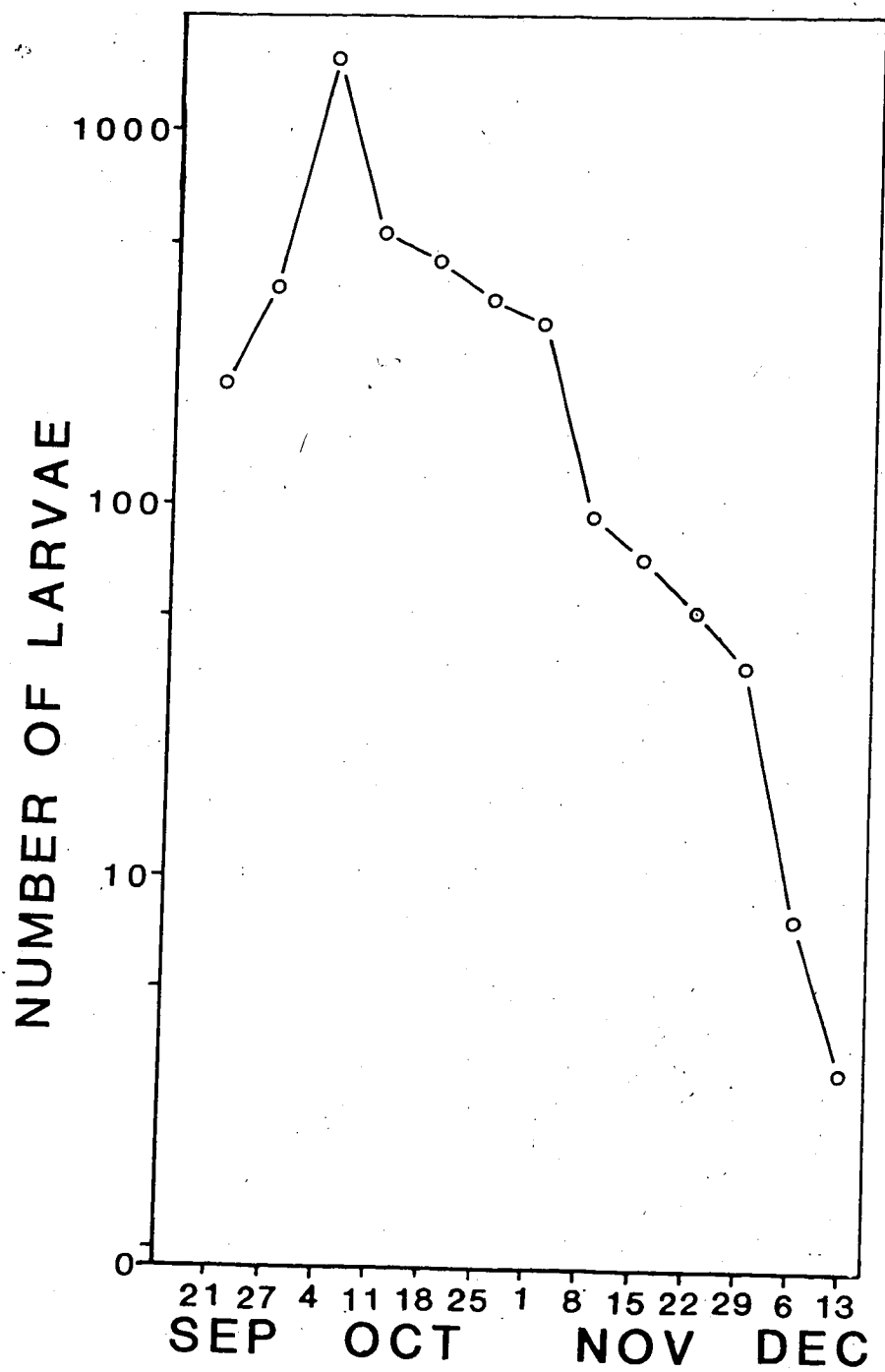
Figure 11. Changes in mean numbers of <u>Dermacentor albipictus</u> larvae

collected by flagging along six game trails at Elk Island

National Park, Alberta, 1981 (O) and 1982 (●). The same

trail sites were used in both years.
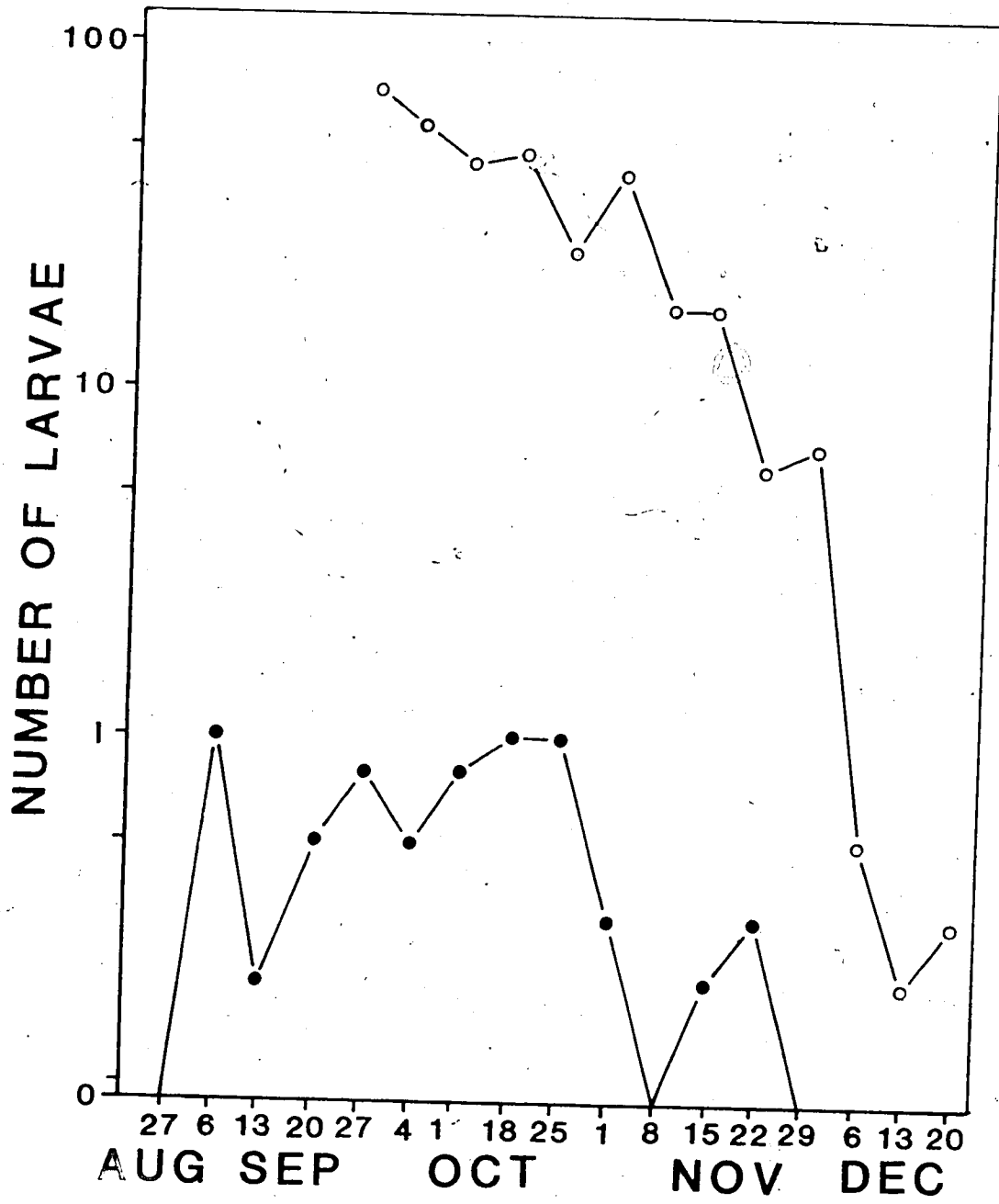
Figure 12. A clump of _Dermacentor albipictus_ larvae in Elk Island

National Park, Alberta. (Photo by M. Pybus).

Table 3. Height and size of clumps of larval _Dermacentor albipictus_ in the aspen habitat in Elk Island National Park, Alberta, 1981.

| Vegetation | Importance Value Rank | # Clumps Measured | Clump | | | | $\bar{x}$ Height of Vegetation Without Larval Clumps (cm) |
| | | | Height (cm) | | No. of larvae | | |
			$\bar{x}$	Range	$\bar{x}$	Range	
Aspen (_Populus_ spp.)	13	31	131	58-400	221	10-1000	140
Grass (_Graminae_)	8	36	61	20-100	99	10-500	77
Rose (_Rosa_ spp.)	6	24	82	57-132	173	50-700	86
Beaked Hazelnut (_Corylus cornuta_)	9	10	106	75-130	208	50-1000	108
Raspberry/Blackberry (_Rubus_ spp.)	8	5	86	34-160	147	25-200	106

Table 4. Vegetation preferences of larval <u>Dermacentor</u> <u>albipictus</u> in experimental plots on the roof of the Biological Sciences Center, University of Alberta, 1981 and 1982.

Vegetation	1981[a]		1982[b]	
	# larvae	(%)	# larvae	(%)
Aspen (<u>Populus</u> spp.)	3683	(26.1)	173	(8.2)
Birch (<u>Betula</u> <u>papyrifera</u>)	214	(1.5)	---	---
Rose (<u>Rosa</u> spp.)	900	(6.4)	---	---
Spruce (<u>Picea</u> <u>mariana</u>)	49	(0.4)	---	---
Applicator stick	---	---	51	(2.4)
Beaked hazelnut (<u>Corylus</u> <u>cornuta</u>)	---	---	468	(22.3)
Grass (Graminae)	---	---	316	(15.0)
Side of tub	9289	(65.7)	1094	(52.1)
Total Recovery	14135	(58.9)	2102	(17.5)

[a] 24,000 larvae released onto 8 plots.

[b] 12,000 larvae released onto 6 plots.

Activity of larvae in the field varied greatly with air temperature. At temperatures above 10°C, all larvae were active and questing. Between 5 and 10°C, larvae were activated by jarring the twig, creating a shadow, or exhaling near them. At temperatures from 0 to 5°C, larvae could be activated by repeated exhalation, which usually took less than 15 sec. Between 0 and -8°C, larvae had to be warmed by exposure to human skin temperature for two to three min before activation occurred. At temperatures below -8°C, the larvae became activated only after exposure to human skin temperature for 15 to 60 min.

For the first 7-10 days after release, larvae in the vegetation plots on the roof avoided high light intensities. Most larval clumps (90-100%) were on the shaded side of upright stems and artificial supports, or on the underside of horizontal leaves and branches. The clumps moved continously to stay in shadow, especially on upright stems and supports. As the temperature declined in autumn, larval activity declined, resulting in stabilization of both clump size and position. Larvae in the field were observed to behave in a similar manner.

E. Experimental infestations of captive moose

The experimentally infested calves apparently handled the infestation with 30,000 *D. albipictus* well as four of the five mass-infested moose (MO 46,50,55 and 71) and all trickle-infested calves (MO 59, 68, and 69) survived. MO 60 died early in the experiment on 18 November, 1982 due to severe emaciation of unknown etiology. MO 68 developed a mild case of pneumonia in late April, 1982, but was treated and appeared to recover.

Only one of the two reinfested yearling moose (MO 50 and 55) survived the second infestation. The survivor (MO 50) became anorexic in November and lost 95 kg by June, but is currently (July, 1983) doing better. The other reinfested yearling died on 28 November, 1982 of a chronic, abcessing pneumonia and emaciation. *Corynebacterium pyogenes*, which might have been acquired during the initial tick infestation, was isolated from the lungs.

The uninfested calf (MO 48) survived the first experiment. He was used as an uninfested control in 1982, but died on 15 November of severe emaciation of unknown

etiology.

All calves were in good health at the onset of the infestation and gained weight throughout most of the experiment. Weight changes per week declined from January to May for both mass- and trickle-infested animals as well as the control (Fig. 13a). Food consumption for all calves generally increased over the course of the experiment (Fig. 13b), probably as a result of the continual weight gain of all calves. The control calf generally consumed more feed per week but gains per week and gains per kg feed consumed were approximately the same as the infested calves (Fig. 13c).

Summaries of the weekly counts of ticks during the infestations of the eight moose calves and two yearlings are shown in Appendix 7. Because no apparent differences were detected in timing of instar molt and duration of each instar between mass-infested calves in 1981 and 1982, results were combined. In general, development of *D. albipictus* from larvae to nymphs on trickle-infested moose was chronologically earlier than on mass-infested moose. Development from engorged nymphs to engorged females was similar on both groups of moose due to the long period of nymphal inactivity (Fig. 14). Within 10-14 days post-infestation, all larvae had fed and molted to nymphs. Nymphs dominated the tick population of all moose from October to early January. Adult males appeared in small numbers on almost all calves by late November, but the large increase in numbers of males did not start until January. Males preceded females by 20-30 days and persisted much longer, comprising 100% of the ticks counted in the last two to three weeks of the infestation. Adult females appeared in late January and peaked in numbers in late March and early April on both groups of calves. Engorged females appeared in late February on both mass and trickle-infested calves and tended to peak in numbers in mid-April. A peak in female numbers was usually followed 7 to 10 days later by a peak in numbers of EF, implying an engorgement period of about 10 days. The length of the EF drop-off period was approximately 9-10 weeks for calves in both infestation groups.

The timing of appearance and duration of larvae, engorged larvae, nymphs, and engorged nymphs on the reinfested yearlings was similar to those of the primary infestations. Adult males and females did not appear on the surviving yearling until 4-6 weeks after the initial appearance of adults on the calves of either primary infestation

Figure 13. Mean weight changes and food consumption of moose calves

experimentally infested with Dermacentor albipictus, 1981-

82 and 1982-83. O – control (n=1), □ – mass-infested

(n=4), ● – trickle-infested (n=3).
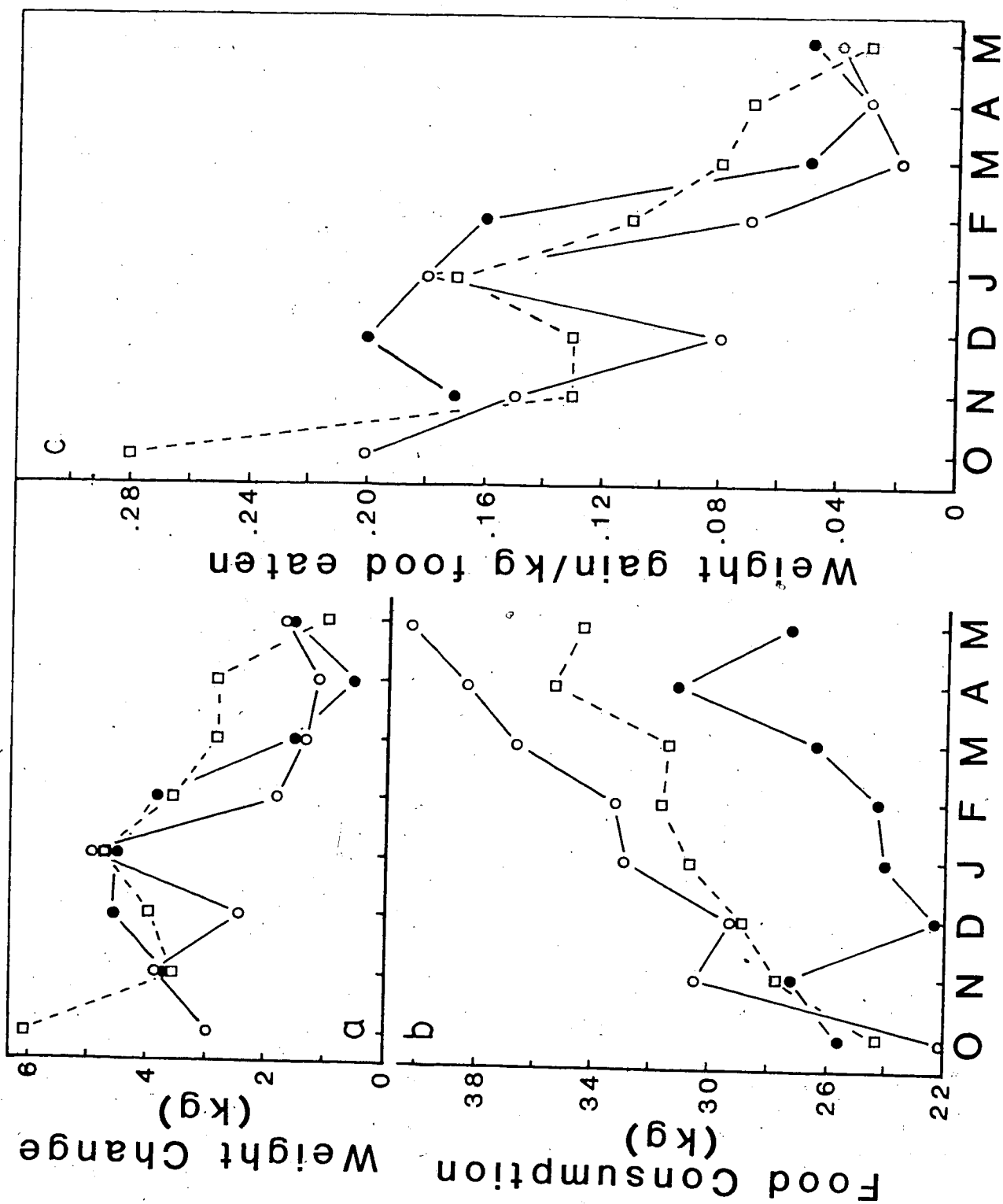
Figure 14. Comparison of instar changes of <u>Dermacentor</u> <u>albipictus</u>

on mass- and trickle-infested moose calves, 1981 and 1982.

O= larvae, ● = engorged larvae, □ = nymphs,

■ = engorged nymphs, ◇ = males, △= females, ▲=engorged

females.
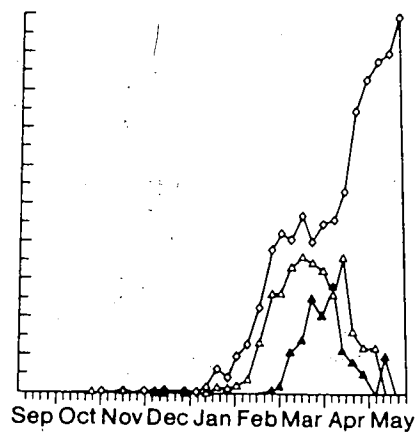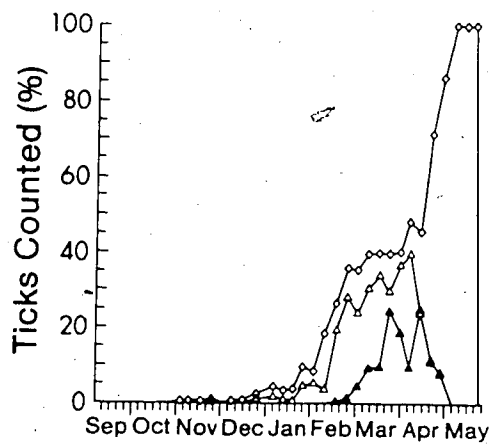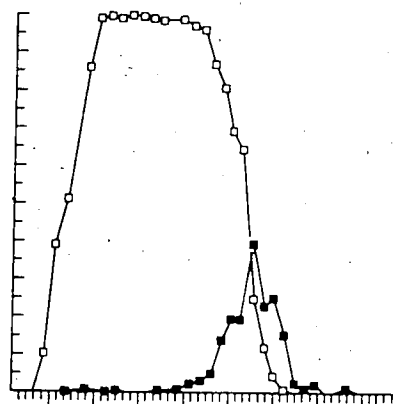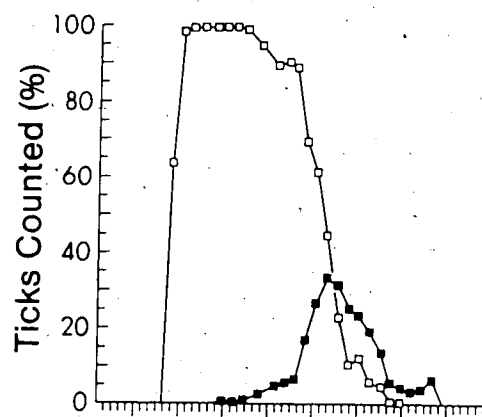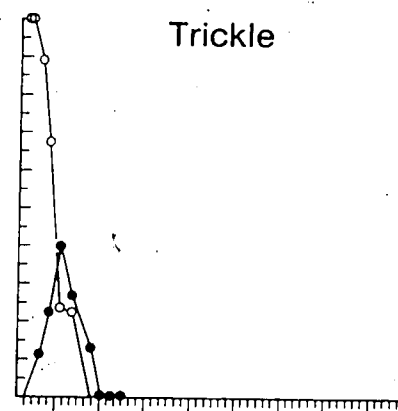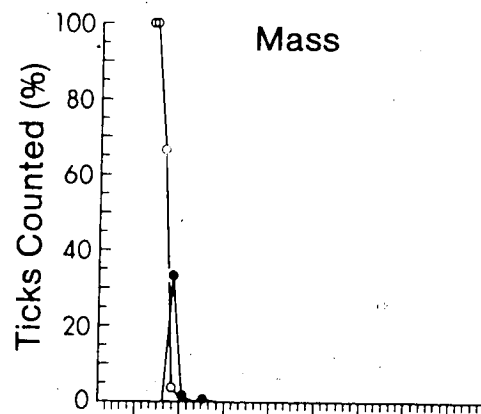
technique. The appearance and duration of EF on this yearling was similar to both groups of calves.

The control moose (MO 48) acquired 19 ticks in 1981. All were removed as soon as they were discovered. He did not acquire any ticks in 1982, although he died very early in the experiment.

Only a small percentage of the 30,000 larval *D. albipictus* put onto each experimental moose in either infestation technique were recovered as EF ($\bar{x}$=1.5%). A total of 1673 EF ($\bar{x}$=419 EF per moose) was picked up from the bedding of the four mass-infested calves. A total of 1447 EF ($\bar{x}$=482 per moose) was picked up from the bedding of the three trickle-infested calves. Only 223 EF were picked up from the reinfested yearling, possibly attributing to the efficiency of his early grooming behavior.

EF did not drop at a constant rate from experimental moose. The major peak of EF drop-off was in late March regardless of year or infestation technique (30 March, 1982 and 28 March, 1983) (Fig. 15). For the mass-infested calves, an average of 53% of the total number of EF collected was dropped by the end of the major peak in late March, 77% by 15 April, and 99.5% by 1 May while for the trickle-infested calves, an average of 62% of the total number of EF collected was dropped by the end of the major peak in late March, 90% by 15 April, and 99.7% by 1 May. The reinfested yearling dropped only 13% of the total number of EF collected by the end of the major peak in late March, 45% by 15 April and 93% by 1 May (Fig. 16).

No difference was found in the average weight of EF between mass- and trickle-infested calves ($\bar{x}$=517 and 535 mg, respectively). The weight of EF from all calves decreased over time (Fig. 17), and no difference was observed in the rate at which EF weight decreased between mass- and trickle-infested calves (covariance, F=0.0016, p=0.968). In contrast, EF from the reinfested yearling increased in weight over time (Fig. 16), possibly due to his poor condition, or to the relatively low numbers of ticks that ___ throughout the experiment allowing more complete engorgment of EF.

Movements of ticks on experimental moose varied with instar, but were similar on ___ and trickle-infested calves (Fig. 18). Larvae moved only short distances from the ___estation site before attaching and feeding. Nymphs moved extensively over most of the body, but tended to aggregate at the top of the hump and rump. Adults also

Figure 15. Mean numbers of engorged female <u>Dermacentor</u> <u>albipictus</u> collected

from experimentally infested moose calves, 1982 and 1983.

(O) mass-infested, <u>n</u> = 4; (●) trickle-infested, <u>n</u> = 3.
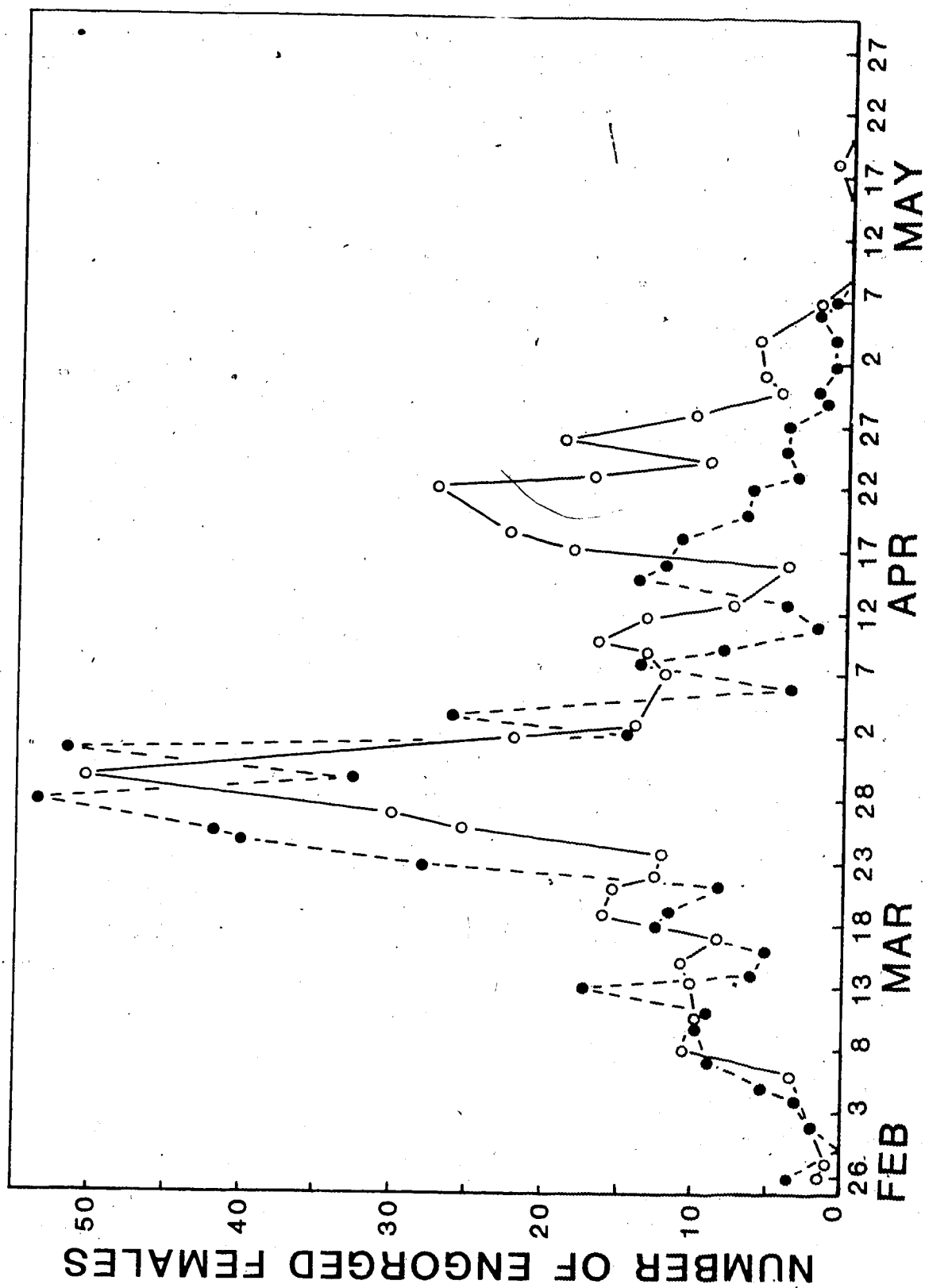
Figure 16. Changes in numbers and weight of engorged female
Dermacentor albipictus collected from the re-infested
yearling moose, 1983. ● = number of engorged females
collected, O = engorged female weight.

ENGORGED FEMALE WEIGHT (g)

NUMBER OF ENGORGED FEMALES

FEB MAR APR MAY
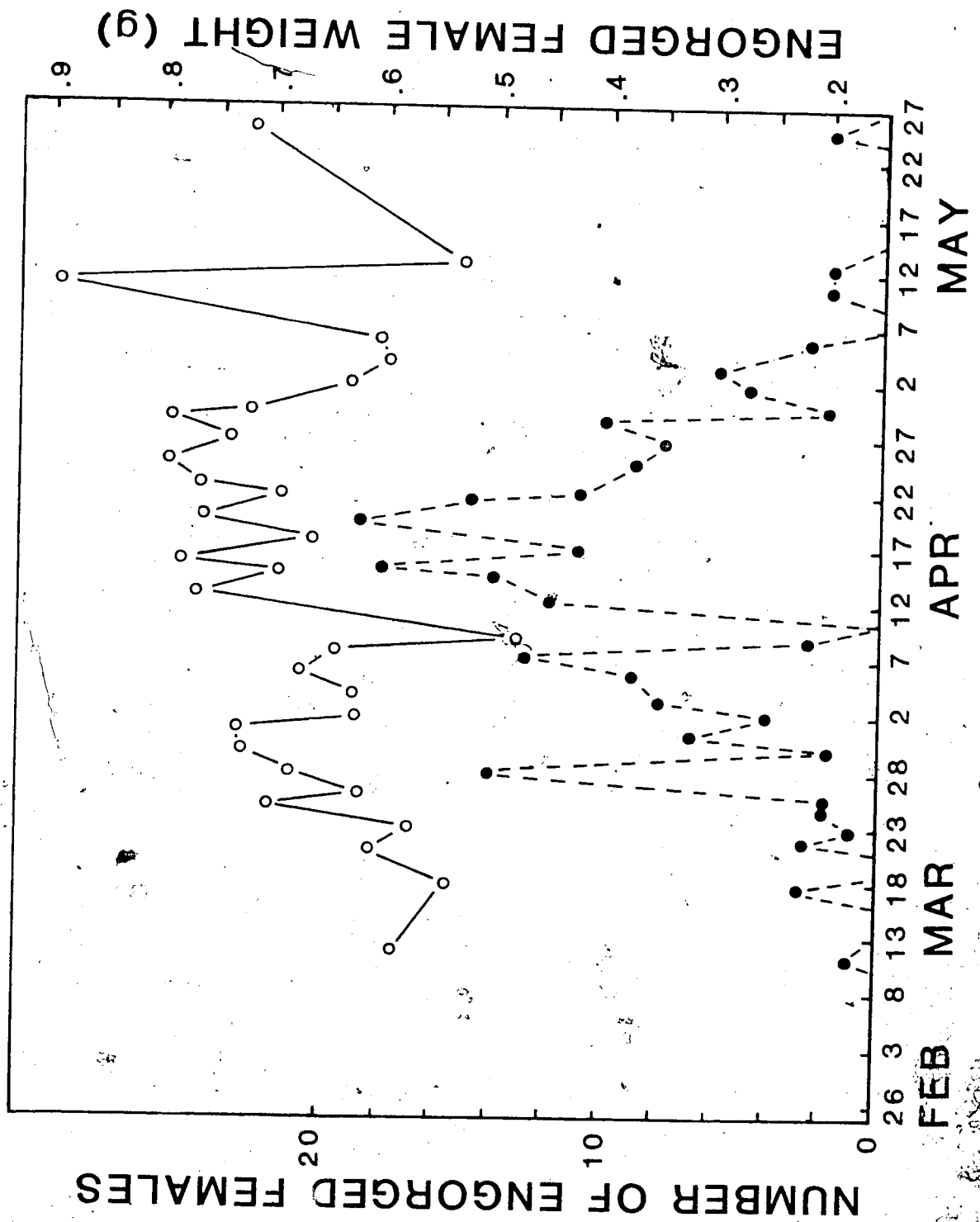
Figure 17. Mean weight changes of engorged female Dermacentor albipictus collected from experimentally infested moose calves, 1982 and 1983. (O) mass-infested, n = 4; (●) trickle-infested, n = 3.
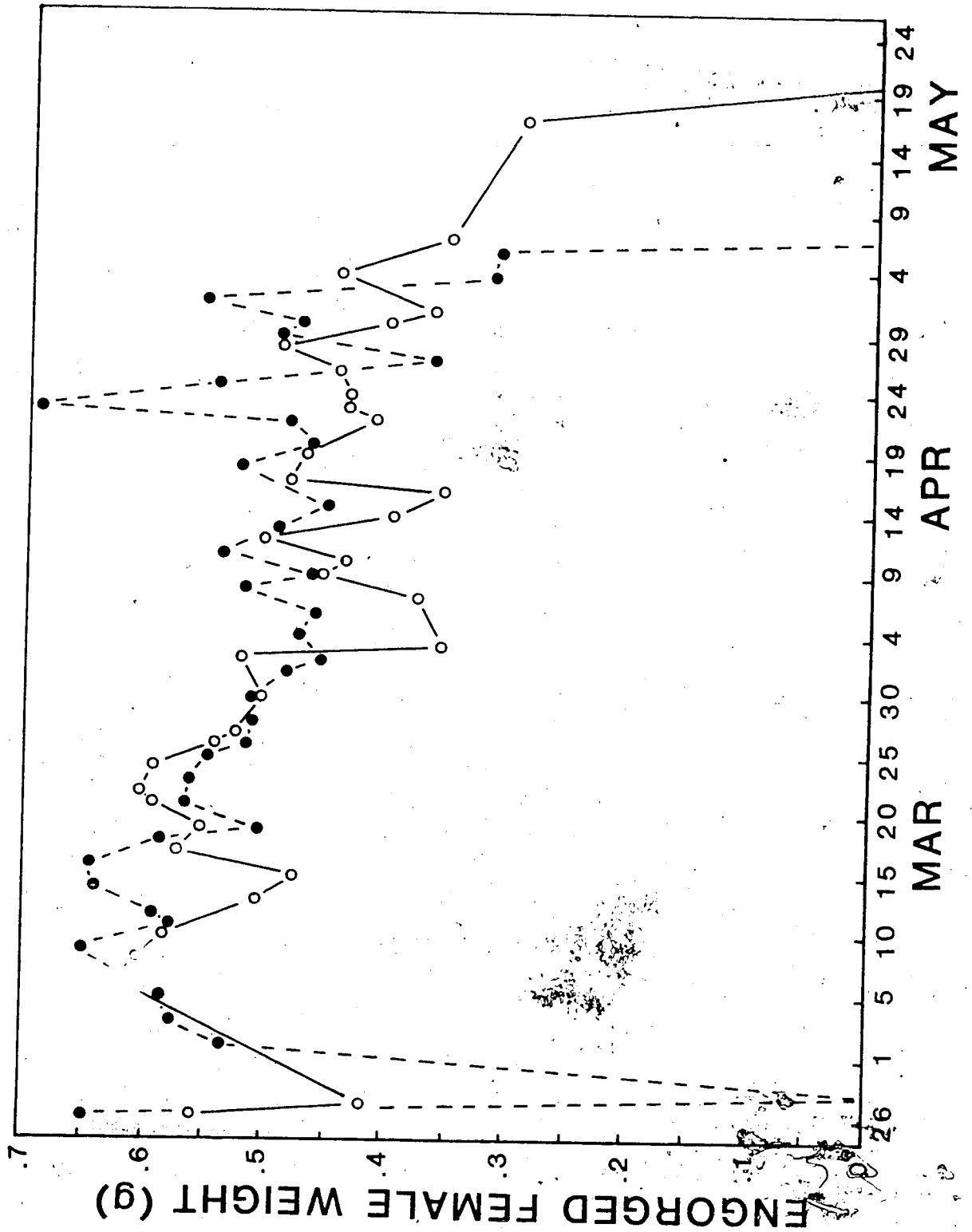
Figure 18. Representative summaries of density, movements of Dermacentor

albipictus, and grooming response by experimentally infested

moose calves. Tick density: ☐ no ticks, ▨ low (1-5/cm),

⬖ moderate (5-10/cm), ■ high (10/cm).

Grooming: ☐ normal hair, ▨ chewed or licked hair, ⬖ rubbed

hair more than half normal lenght, ▦ rubbed hair less than half

normal lenght, ■ bare.

	MASS-INFESTED		TRICKLE-INFESTED	
	TICK DENSITY	GROOMING	TICK DENSITY	GROOMING

SEP 15

OCT 15

NOV 15

DEC 15

JAN 15

FEB 15

MAR 15

APR 15

MAY 15
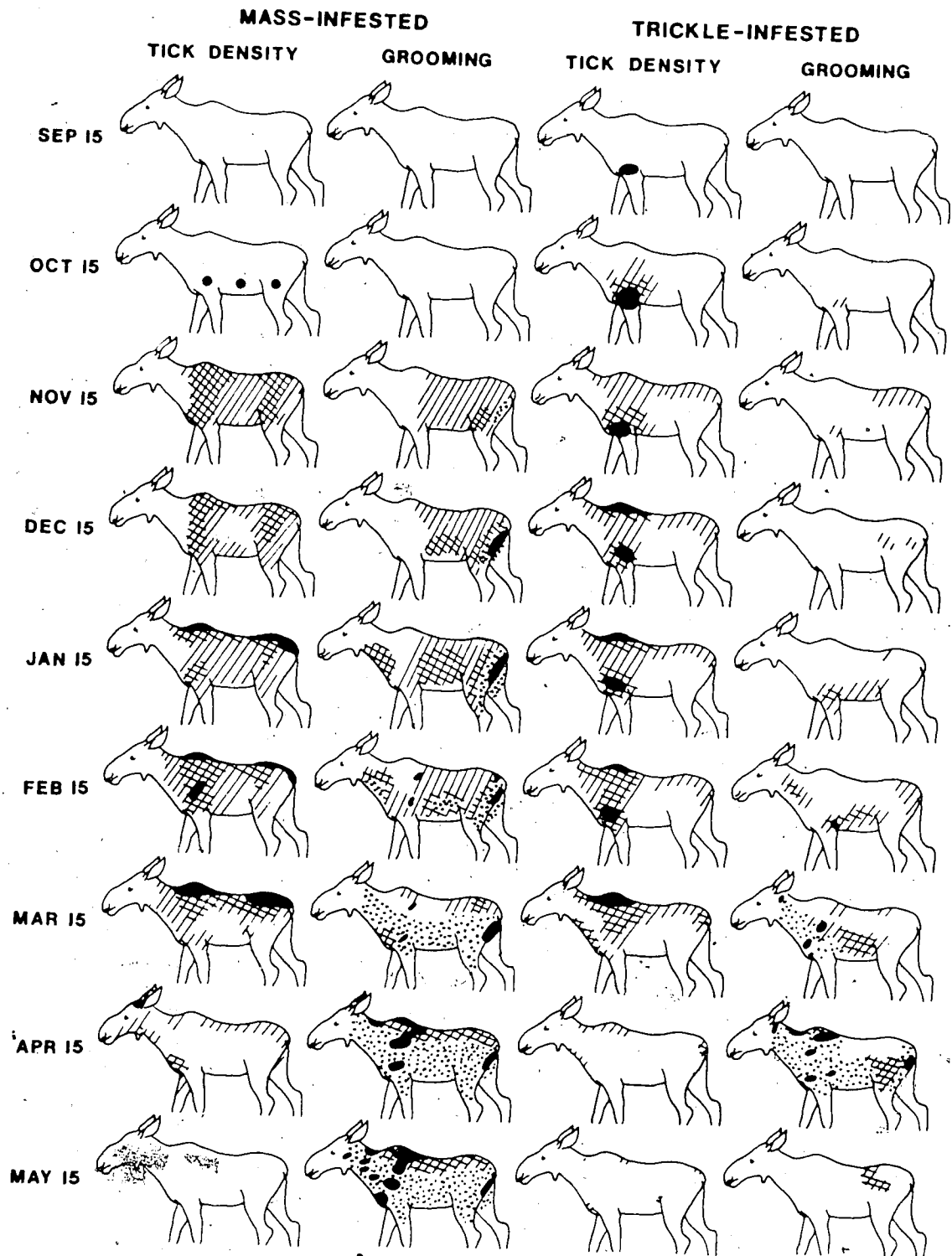
congregated at these locations, but spread downward from the top of the hump onto the shoulder.

Movements of ticks in relation to or in response to grooming were not clear. The aggregations of nymphs and adults were in relatively inaccessible areas to grooming, however, it was impossible to determine whether or not the movement was caused by grooming, due to site selection by ticks, or to other factors such as secretion of assembly pheromones by the different instars (Sonenshine et al. 1982).

Due to the initial infestation method and site, the location of ticks over time differed between mass- and trickle-infested calves (Fig. 18). Ticks on trickle-infested calves did not reach the rump area until about November (2 months post-exposure) and did not reach the densities in this area as seen on mass-infested calves.

There was no apparent relationship between tick density and areas groomed by moose. The first area of hair loss, with the exception of the thigh on mass-infested moose, was the side (Fig. 18), although tick density was very low in this area when grooming started. Grooming on the shoulder and hump regions began/coincided with the appearance of engorged nymphs, males, and females in January. No instar could be clearly demonstrated to initiate grooming, but the increased irritation due to the greater mobility and feeding of nymphs and adults seemed to increase the rate of grooming and subsequent hair loss.

F. Reproduction of engorged female ticks

In 1982, EF from MO 46 and MO 50 (both mass-infested) were consistently lighter than those from MO 55 (also mass-infested) (F=72.45 and 55.84, each $p<.0001$). The mean weight of EF from individual moose for each experimental replicate was not significantly different, therefore, data on EF from all three experimental moose were combined.

In 1983, mean EF weight was not different between MO 59 and 68 (both trickle-infested) (F=1.04, $p=.309$), but EF from MO 69 and 71 (trickle- and mass-infested, respectively) were lighter than EF from MO 59 and 68 (F=11.04 and 6.90, $p=.0009$ and .0087, respectively). The mean weight of EF from each moose for each experimental replicate was not significantly different and data from EF from the four calves were

combined for the reproductive studies under field and laboratory conditions. Data on EF from the reinfested yearling (MO 50) were kept separate from data on EF from the four calves for laboratory reproductive studies.

All reproductive experiments included replicates along a time series. A detailed comparison of reproductive parameters within treatment groups is provided in Appendix 8 to show changes that occurred in response to the differences in timing of EF drop-off. Comparisons between treatment groups are provided to show changes in reproductive parameters attributed to experimental conditions. Although EF survival was affected by many factors, all EF died after completing oviposition.

A small percentage (5-6%) of the EF used in these reproductive experiments did not oviposit properly. These EF appeared to begin oviposition concurrently with EF in the same treatment group, but did not lay eggs. Most extruded a sticky, pale yellow fluid from the genital aperture and appeared to undergo a similar weight loss pattern to EF that laid eggs. Some of these EF were fixed in gluteraldehyde for examination with a Transmission Electron Microscope. Results are still incomplete, but it is possible that these EF were genetically or physiologically abnormal and could not lay eggs.

Reproduction of engorged females under laboratory conditions

Detailed summaries of the results of the reproductive experiments with EF under various laboratory conditions (see Table 1) are shown in Appendix 8. General comments on trends and patterns observed in these experiments are presented here.

Survival of EF was generally fairly high and remained relatively constant over successive drop periods for constant and cold stress treatments, but not under fluctuating conditions (Appendix 8). The length of the preoviposition period declined with successive drop periods in all treatments with more than two replicates for both successful and unsuccessful EF (Fig. 19 and Appendix 8). Most other reproductive parameters measured such as incubation period, number of eggs laid, percent hatch, larval survival, and reproductive efficiency index, remained fairly constant between drop periods for both successful and unsuccessful EF, although unsuccessful EF generally had a lower reproductive output than successful EF. Total production was usually the only parameter that was significantly related to EF weight, although REI and EF weight were significantly

Figure 19. Changes in the preoviposition period of engorged female

Dermacentor albipcitus under various laboratory conditions,

1982 and 1983.
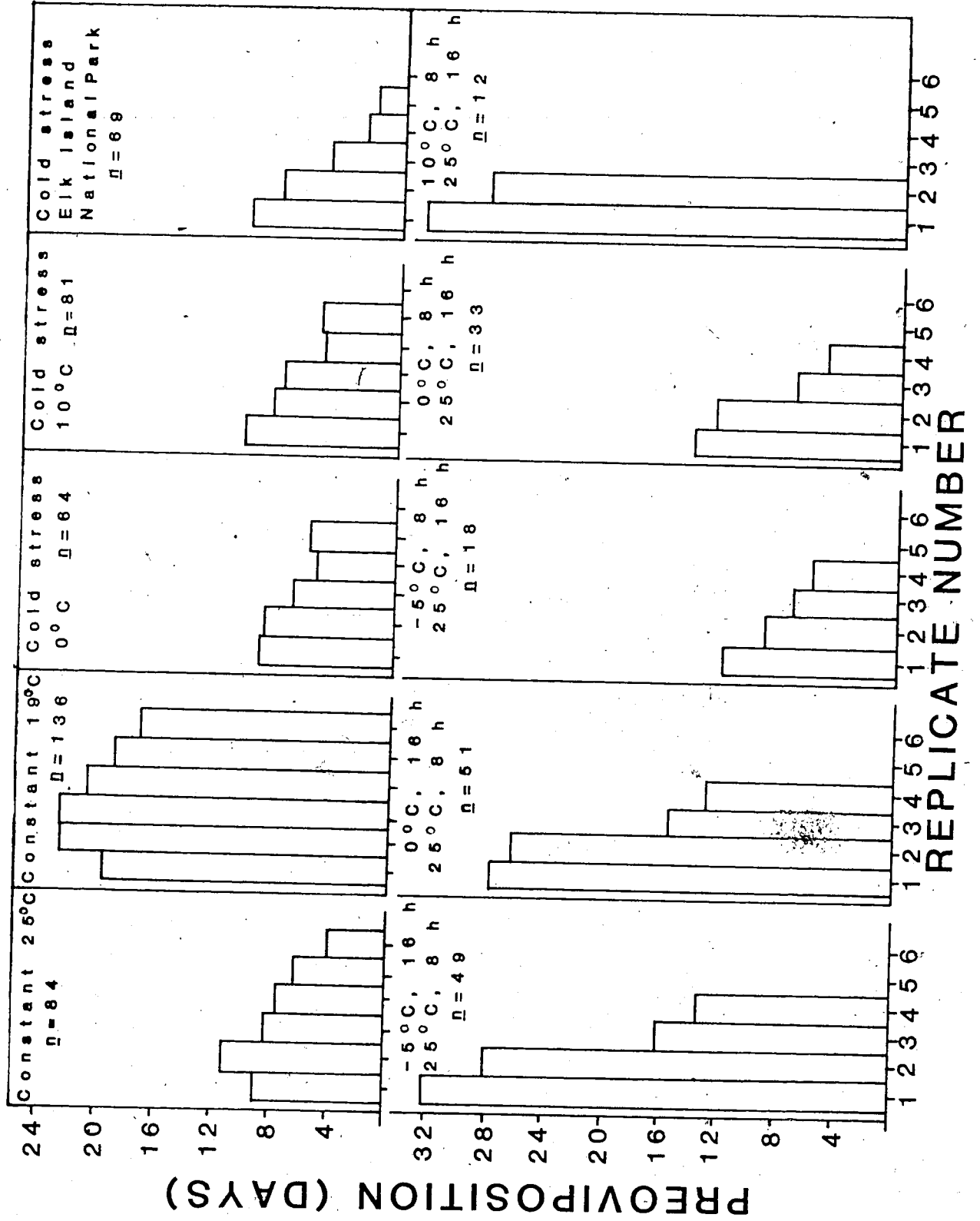
related in a few treatment groups (Appendix 8). Percent hatch varied greatly with experimental conditions, but larval survival decreased dramatically after approximately 120 days at 25°C from approximately 85% to 15-25% in all cold stress and constant temperature treatments. No larvae survived the fluctuating conditions.

Reproduction of engorged females under field conditions

Determination of the chronology of reproduction and reproductive potential of EF *D. albipictus* under field conditions was one of the major objectives of this study. In general, the events in the reproductive cycle of EF were influenced by environmental variables and, therefore, were somewhat predictable. Productivity varied between habitat types, suggesting a favored or at least a more favorable habitat was available in the open-canopied sites.

Survival of EF (see definition p. 7) increased from early March to early May in both 1982 and 1983 (Tables 5 and 6), but the rate of survival from early March to late April was not different between 1981 and 1983 (covariance, $F = 5.944$ $p > 0.05$). Survival of EF in all three habitats in both 1982 (Table 5) and 1983 (Table 6) was greatly influenced by snow melt which occurred around 24 April, 1982 and 10 April, 1983. Survival of EF put in cages prior to snow melt was low, averaging 10% and 11% for 1982 and 1983, respectively, but survival after snow melt (to 30 April) averaged 61% and 60% for 1982 and 1983, respectively.

With the exception of the aspen habitat in 1982, the mean proportion of EF that survived to oviposit in the three habitats was similar between 1982 (29%, 15%, and 25% for the bog, aspen, and grassland, respectively), and 1983 (29%, 29%, and 33% for the bog, aspen, and grassland, respectively) for comparable dates, and averaged 27%. Hovever, overall survival of successful EF in the bog and grassland was almost three times that of EF in the aspen in 1982 from the onset of oviposition (42%, 35%, and 45% for the bog, aspen, and grassland, respectively) (Table 5) to the time of hatching (34%, 37%, and 13%, respectively) (Table 7), implying a marked mortality rate in the aspen habitat after initiation of oviposition. Survival of EF was significantly lower in the aspen than in the bog or grassland (x^2, 2 df = 13.2, $p < 0.05$).

Table 5. Changes in the preoviposition period and survival of engorged female (EF) <u>Dermacentor albipictus</u> under fiel condisitions in three habitat types in Elk Island National Park. Alberta, 1982.

Location	Date Expt. Began	No. of EF	EF Survival		Preoviposition Period (days $\pm$ 1 SD)[b]
			No.[a]	%	
BOG	3/14	4	1	25.0	87.0
	3/27	18	2	11.1	72.0
	4/10	18	1	5.6	60.0
	4/24	18	13	72.2	44.7 $\pm$ 4.4
	5/8	10	9	90.0	28.8 $\pm$ 6.8
	5/22	6	3	50.0	14.5 $+$ 0.7
	ALL	74	28	42.3	40.6 $\pm$ 16.8
ASPEN	3/14	9	0	0.0	----
	3/27	18	1	5.6	76.0
	4/10	18	2	11.1	59.0
	4/24	18	8	44.4	44.7 $\pm$ 15.3
	5/8	10	9	90.0	26.0 $\pm$ 7.4
	5/22	5	3	60.0	19.0
	ALL	78	23	35.2	39.2 $\pm$ 18.6
GRASSLAND	3/14	5	0	0.0	----
	3/27	18	1	5.6	----
	4/10	18	4	22.2	60.0 $\pm$ 3.1
	4/24	18	12	66.7	38.3 $\pm$ 10.2
	5/8	10	10	100.0	29.1 $\pm$ 8.0
	5/22	5	5	100.0	17.8 $+$ 0.5
	ALL	73	32	44.8	36.2 $\pm$ 15.3

[a]Number of engorged females that survived and laid eggs as of 20 June.
[b]Calculated for successful engorged females only.
Snow melt occurred around 24 April.

Table 6. Changes in the preoviposition period and survival of engorged female (EF) _Dermacentor albipictus_ under field conditions in three habitat types in Elk Island National Park, Alberta, 1983.

Location	Date Expt. Began	No. of EF	EF Survival		Preoviposition Period (days $\pm$.1 SD)[b]
			No.[a]	%	
BOG	3/6	12	0	0.0	---
	3/19	46	8	17.4	77.4 $\pm$ 5.5
	4/2	48	6	12.5	63.8 $\pm$ 5.9
	4/16	48	25	52.1	49.5 $\pm$ 3.5
	4/30	33	21	63.6	36.6 + 5.4
	ALL	187	60	29.1	48.5 $\pm$ 14.0
ASPEN	3/6	11	1	9.1	97.0
	3/19	50	3	6.0	73.3 $\pm$ 6.4
	4/2	48	7	14.6	57.6 $\pm$ 3.6
	4/16	50	34	68.0	49.8 $\pm$ 5.5
	4/30	33	15	45.5	34.9 + 4.9
	ALL	192	60	28.6	50.0 $\pm$ 12.5
GRASSLAND	3/6	12	0	0.0	---
	3/19	48	3	6.3	77.0 $\pm$ 3.5
	4/2	48	14	29.3	65.4 $\pm$ 8.7
	4/16	47	24	51.0	45.2 $\pm$ 4.5
	4/30	26	20	76.9	34.8 + 4.6
	ALL	181	61	32.7	48.0 $\pm$ 14.3

[a] Number of engorged females that survived and laid eggs as of 20 June.
[b] Calculated for successful engorged females only.
Snowmelt occurred around 10 April.

Table 7. Reproductive parameters of engorged female (EF) <u>Dermacentor</u> <u>albipictus</u> under field conditions in three habitat types in Elk Island National Park, Alberta, 1982.

Parameter	Habitat Type		
	Bog	Aspen	Grassland
No. of EF	74	78	73
No. (%) EF that survived	25(34)	10(13)	27(37)
Preoviposition period (days)	41 $\pm$ 17[*]	39 $\pm$ 19	36 $\pm$ 15
Incubation period (days)	81 $\pm$ 12	106 $\pm$ 21[c]	79 $\pm$ 10
Total production (eggs/EF)	3227 $\pm$ 1590	3013 $\pm$ 1319	3152 $\pm$ 1361
% eggs hatched (95% CI)[b]	51(39, 62)	23(9, 41)[c]	59(44, 72)
% larval survival (95% CI)[b]	14(6, 26)	6(1, 18)[c]	36(21, 51)
Reproductive efficiency index (eggs/g EF)	6029 $\pm$ 1733	5579 $\pm$ 2119	5897 $\pm$ 2179

[a] Number of engorged females that survived and laid eggs.

[b] Statistical tests run on arcsin transformations of these values.

[c] Using an F-test for linear combinations of means, these values are significantly different ($p \leq 0.05$).

[*] mean $\pm$ 1 SD.

Although the preoviposition period was not significantly different in the three habitat types in 1982 (Table 7), it decreased with successive drop periods within each habitat type (r=-0.9199, -0.9214, -0.8604, each $p<.0002$ for bog, aspen, and grassland, respectively) (Table 5) and in 1983 (r=-0.9426, -0.9014, -0.9055, each $p<.0001$ for the bog, aspen, and grassland, respectively) (Table 6). In spite of the changing preoviposition period, the chronological mean for the onset of egg laying for EF in all habitats and all drop periods was 7 June, 1982 and 5 June, 1983 (Fig. 20).

In most other reproductive parameters monitored in 1982, the aspen habitat appeared detrimental to successful reproduction (Table 7). The incubation period did not change over time, but was over 20 days longer in the aspen forest than the bog or grassland. Percent egg hatch and larval survival from hatching to 15 November, 1982 in the aspen forest was half that in the bog or grassland.

No reproductive parameters except preoviposition period were correlated with the date the EF were placed in the field. Total production was significantly correlated with EF weight in the bog and grassland (r=0.772 and 0.468, $p<.0001$ and .0139, respectively) but not in the aspen (r=0.458, $p=.1827$). No other reproductive parameters were related to EF weight.

Twenty-six EF, over half of which were in the aspen forest habitat, laid eggs that failed to hatch (Appendix 8), although no cause was determined.

Comparisons of reproduction between various experimental conditions with constant 25°C

Because most reproductive studies of ticks are done under constant temperature and relative humidity conditions, data from all treatments used in this study were compared to data from the constant 25°C control treatment to determine if the variations outlined above were due to the non-standard and/or suboptimal conditions. All comparisons were based on mean values for the reproductive parameters of EF in each of the treatment groups. Important variations and general trends are identified where appropriate.

The mean weight of EF that laid successful eggs was variable, but was usually around 550 mg in all treatment groups. The mean weight of the EF at constant 25°C was

Figure 20. Chronological onset of oviposition of engorged female
Dermacentor albipictus in three habitat types in Elk
Island National Park, Alberta, 1982 and 1983.
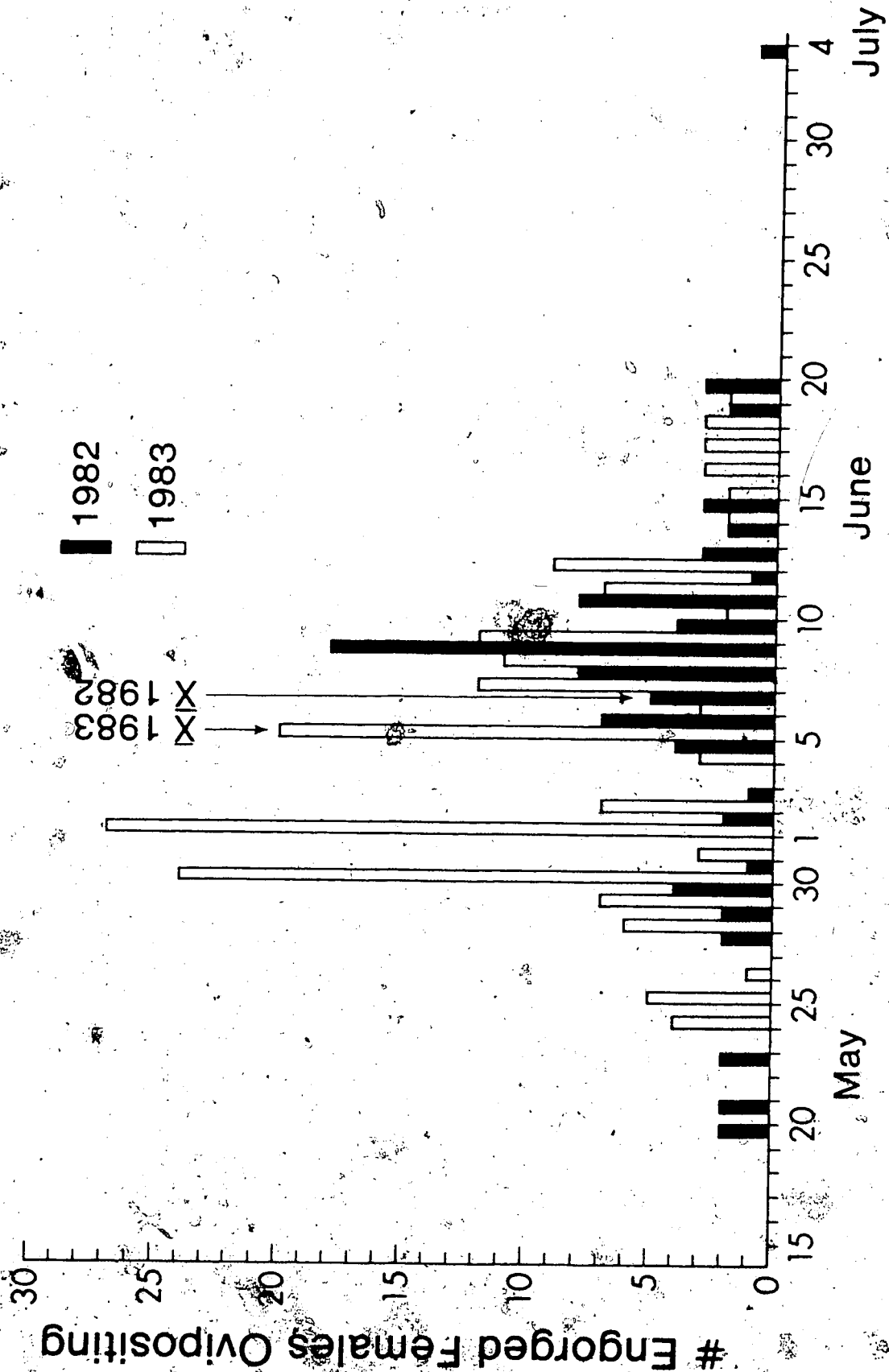
470 mg, the only value less than 500 mg, possibly reflecting the more optimum conditions for survival and reproduction in this treatment group. The minimum weight needed for successful reproduction was about 200 mg and did not vary greatly between treatment groups.

Field conditions versus constant 25ºC

Survival and reproduction of EF under field conditions was poorer than under constant 25ºC (Table 8). EF survival was lower, preovipostion and incubation periods longer, and reproductive output and efficiency lower.

Cold stress versus constant 25ºC

Cold stresssing EF had a stimulatory effect on productivity and reproductive efficiency. The length of' the reproductive cycle was generally similar between all cold stress treatments and the control. EF survival, preoviposition period, and larval survival decreased with severity of the cold stress (Table 8).

Fluctuating conditions versus constant 25ºC

Survival and reproductive output of EF under fluctuating conditions was markedly poorer than under constant 25ºC (Table 8). EF survival was lower, preoviposition and incubation periods longer, and reproductive output and efficiency lower.

Comparisons between field, cold stress, and fluctuating conditions

Comparisons between reproductive parameters of EF under field, cold stress, and fluctuating conditions are complicated and yield few distinctive patterns. Small sample sizes of EF in some treatment groups only add to the problem. The major pattern observed was that cold stressed EF generally had a higher survival and productivity than EF in other treatment groups (Table 8).

Reproduction of engorged females from other hosts under constant 25ºC

There were few differences in reproductive parameters of EF from free-ranging wapiti, white-tailed deer, and moose (Table 9). Mean weights of EF were different ($\bar{x} \pm SD$ = 181±160 mg, 405±187 mg, and 509±238 mg for wapiti, white-tailed deer, and moose, respectively), but EF from wapiti were lightest due to removal from the host prior to complete engorgement. Survival of EF from moose was lower (40%) than survival of EF from wapiti and white-tailed deer (94% and 89%, respectively). As reported

Table 8: Comparisons of reproductive parameters of engorged female (EF) Dermacentor albipictus from experimental moose in the 11 treatment groups, 1982.

Treatment Group and conditions	No. of EF	EF Survival[a] No.	%	Preoviposition (days)	Incubation (days)	Total Production (eggs/EF)	Percent of Eggs that Hatch (95% CI)[b]	Percent of Larvae that Survive (95% CI)[b]	Reproductive Efficiency Index (eggs/g EF)
Constant 25°C	141	84	60	8.3 ± 3.6*	36.8 ± 4.8	3732 ± 2147	97(95, 98)	16(14, 22)	7531 ± 1961
Cold Stress −22°C,25°C	110	0	0	---	---	---	---	---	---
0°C,25°C	106	64	60	7.5 ± 4.4	37.7 ± 3.3	4408 ± 1591[d]	98(96, 99)	88(80, 95)[d]	8093 ± 1570[d]
10°C,25°C	115	81	70	8.3 ± 5.0	37.5 ± 2.8	4344 ± 1577[d]	99(98, 99)[d]	96(84, 99)[d]	8060 ± 1310[d]
Field,25°C	155	69	45	5.5 ± 3.5[cd]	37.2 ± 4.1	4456 ± 1365[d]	98(96, 99)	19(11, 29)	7923 ± 1821
Fluctuating Conditions 16h −5°C 8h 25°C	94	4	4	12.3 ± 3.9	99.0 ± 46.4[d]	3050 ± 481	0.5(0.2, 2)[d]	0[d]	5958 ± 771[d]
16h 0°C 8h 25°C	84	4	5	17.8 ± 2.9[cd]	132.5 ± 2.9[cd]	4305 ± 1567	0.4(−0.7, 2)[d]	0[d]	6968 ± 2236
16h 25°C 8h −5°C	88	18	21	9.1 ± 3.1	66.6 ± 23.8[cd]	3397 ± 652	1(0.4, 3)[d]	0[d]	6198 ± 1189[d]
16h 25°C 8h 0°C	84	33	39	10.2 ± 4.7	58.1 ± 10.8[d]	3469 ± 1039[d]	6(3, 10)[cd]	0[d]	6835 ± 1457
16h 25°C 8h 10°C	75	12	16	31.5 ± 14.8[cd]	98.3 ± 32.3	2645 ± 1079[d]	1	0[d]	4648 ± 1721[cd]
Field Conditions BOG	74	25	34	40.6 ± 16.8[d]	81.4 ± 11.8[d]	3227 ± 1590	51(39, 62)[d]	14(6, 26)	6029 ± 1773[d]
ASPEN	78	10	13	39.2 ± 18.6[d]	103.9 ± 21.2[cd]	3013 ± 1319	23(9, 41)[cd]	6(1, 18)	5579 ± 2119[d]
GRASSLAND	73	27	37	36.2 ± 15.3[d]	79.4 ± 9.6[d]	3152 ± 1361	59(44, 72)[cd]	36(21, 51)[cd]	5897 ± 2179[d]

[a] Numbers of engorged females that survived and laid eggs.

[b] Statistical tests run on arcsin transformations of these values.

[c] Using an F-test for linear combinations of means, these values are significantly different within a treatment group ($p < 0.05$).

[d] Using an F-test for linear combinations of means, these values are significantly different from the control (Constant 25°C)($p < 0.05$).

* mean ± 1SD.

previously, total production was correlated with EF weight (r=0.984, 0.968, and 0.899, each p<.0001, for EF from wapiti, deer, and moose, respectively). The REI was correlated with EF weight for wapiti and moose (r=0.509, 0.621, p=.0048, .0026, respectively), but not for EF from deer.

No significant differences were observed in any reproductive parameters between free-ranging and experimental moose under constant 25°C (Table 9). EF from free-ranging moose produced about 800 more eggs per EF than EF from experimental moose. Larval survival was higher for EF from the experimental moose due to differences in the length of time between hatching and counting (approximately 60 and 170 days for experimental and free-ranging moose, respectively).

Table 9. Reproductive parameters of engorged female (EF) Dermacentor albipictus at constant 25°C from three host species and experimental moose, 1982.

Reproductive parameter	Host species			
	Wapiti	White-tailed Deer	Moose	Experimental Moose
No. of EF	37	28	53	141
No. (%) EF that survived[a]	29(94)	25(89)	21(40)	84(60)
Preoviposition period (days)	6 ± 2*	5 ± 2	7 ± 2[c]	8 ± 4
Incubation period (days)	37 ± 2	38 ± 3[c]	36 ± 2	37 ± 5
Total production (eggs/EF)	1470 ± 1596	3512 ± 1747	4552 ± 2674	3732 ± 2147
% eggs hatched (95% CI)[b]	91(84, 97)	96(90, 100)	97(93, 99)	97(95, 98)
% larval survival (95% CI)[b]	0.01(0.05,0.01)	0.02(0.05,0.01)	0.5(-1, 4)	16(14, 22)[c]
Reproductive efficiency index (eggs/g, EF)	7164 ± 2051[c]	8340 ± 1170	7803 ± 2543	7531 ± 1961

[a] Number of engorged females that survived and laid eggs.

[b] Statistical tests run on arcsin transformations of these values.

[c] Using an F test for linear combinations of means, these values are significantly different ($p \leq 0.05$).

* mean ± 1SD.

IV. DISCUSSION

The winter tick, *Dermacentor albipictus*, is near its northern distributional limit in Alberta. Although 'northern limit' implies unfavorable conditions for both development and high population densities, winter ticks are well established in central Alberta and, therefore, must be well adapted to climatic conditions in the province.

Because the frost-free period is very short, winter ticks must be very efficient in utilizing available habitat areas and favorable environmental conditions to survive, successfully produce larvae off the host, and complete the life cycle. Results of this study suggest that the entire life cycle attuned to the most constant (i.e., photoperiod and temperature) cues available to ensure completion of both parasitic and non-parasitic phases.

The general structure of this discussion will follow the life cycle pattern outlined in Fig. 1. Important aspects in the ecology of the non-parasitic instars of winter ticks include movements of EF, reproductive potential of EF under field conditions, and activities of larvae in autumn. Each of these will be discussed in relation to the findings of the present study and related to the epizootiology of winter tick infestations. Findings of laboratory reproductive experiments and experimental infestations of moose that provide information on the basic biology and transmission of winter ticks will also be discussed. The various aspects of the reproduction and ecology of winter ticks will be summarized and intergrated in a discussion of management implications for moose and ticks in central Alberta.

A. Dispersal of engorged females from moose carcasses

EF *D. albipictus* probably have limited options when they drop from moose in late winter and early spring. Two requirements exist for ensuring completion of the life cycle: the EF must find a suitable site for oviposition and incubation of her eggs, and; she must drop in an area that a moose will frequent the following autumn to enable the larvae to find a host. In this study, finding a suitable site for oviposition did not appear a problem, because most of the EF (87%) recovered were found within 60 cm of the the "artificial" drop site (i.e., moose carcasses).

The presence of the carcass itself probably negated prolonged searching for a suitable oviposition site by EF because it provided the sheltered, shaded environment sought by EF (Balashov, 1972; Diehl et al. 1982). The huge numbers of larvae recovered from vegetation by flagging at carcass sites in autumn tend to confirm this idea. These findings may not reflect what happens when EF drop from live moose and it is possible that dispersal ranges of EF are normally greater than recorded in this study. However, present findings, techniques aside, are similar to those of the few published studies on dispersal of EF of other tick species (Hunter and Hooker, 1907; Patrick and Hair, 1979).

The fact that EF *D. albipictus* did not disperse great distaances is important because the drop site essentially becomes the oviposition site. The distribution of EF is therefore assumed to be directly dependent on moose activity in late winter. Because EF probably have little control over the habitat type into which they drop, environmental factors like temperature appear to be more important in determining the foci for infestations of moose by ticks by affecting the reproductive potential of EF.

B. Reproduction of engorged females under field conditions

The components of the reproductive performance of *D. albipictus* that appear important in the epizootiology of tick infestations on moose and that were examined in this study are: survival of EF, timing of oviposition and egg hatch, numbers of eggs laid, percent egg hatch, and larval survival. All would seem to have been functioning at or near maximum levels and efficiency in EINP during this study to account for average numbers of ticks per moose of over 80,000 (Samuel, unpub.).

Under field conditions, temperature and relative humidity are considered the most important factors influencing tick reproduction (Hixson, 1940; Hitchcock, 1955; Snowball, 1957; Wilkinson and Wilson, 1959; Harley, 1966; Patrick and Hair, 1979). In contrast, the results of this study suggest that photoperiod may be more important than temperature for cueing reproduction, although temperature probably determines the productivity level of EF under field conditions (see below).

Survival of engorged females

Survival of EF under field conditions can be related to two factors: date of snowmelt in spring, and summer weather conditions. The low survival rate of EF prior to

snowmelt in spring may be because the sudden change from body temperature of a moose to ambient temperature at the snow surface is lethal for EF. If the EF can survive this sudden temperature change, it probably cannot survive the long period spent at or near the super cooling point of *D. albipictus*, (-17.5°C, Schmid, pers. comm.), on the snow surface. The peak of EF drop-off from experimental moose occurred from late March to mid-May (Fig. 15) when minimum temperatures ranged from about -5°C to -20°C (Appendix 2 and 3). EF that drop off immediately before or after snow melt survive much better (Tables 5 and 6), perhaps because they are able to acclimatize themselves to the diel fluctuations in temperature that exist, or because minimum temperatures do not fall below the threshold for survival.

The higher mortality of EF after the onset of oviposition in the aspen habitat in 1982 (Table 7) was apparently caused by the dense canopy cover, subsequent shading, and, therefore, lower temperatures (see Fig. 7). It is not clear whether this mortality is to be considered abnormal or was due to environmental conditions that either inhibited oviposition and/or prolonged the preoviposition period to the point of energy deficit and death of the EF.

Patrick and Hair (1975) reported what appears to the opposite: higher survival of EF *D. albipictus* in a forested habitat than in a meadow habitat. The bottom-land oak-hickory forest in their study had very little undergrowth (Semtner et al. 1971a), implying a fairly dense canopy with intense shade. Temperatures were lower, but more stable and relative humidity was higher in the forest than the meadow habitat (Semtner et al. 1971a). The bog and grassland of the present study had temperature and humidity ranges (see Appendix 3) similar to the bottom-land forest of Semtner et al. (1971a). The higher EF survival rates in these habitat types suggests that the meadow habitat used by Patrick and Hair (1975) was too hot and dry and the canopied aspen habitat in the present study too cold (see Fig. 7) for optimum survival of EF *D. albipictus*. Therefore, specific habitat types that are favorable for survivial of winter ticks are probably regional and broad generalizations on habitat specific mortality rates are not possible except in local areas.

The factors that influence EF survival are important in predicting outbreaks of ticks and may be useful in the administration of control eforts. The date of snow melt may be a

useful indicator of potential EF survival rates under field conditions in central Alberta. Because EF survival appeared habitat related, these data should be useful in identifying possible foci for tick infestations of moose. Control efforts may be more successful if directed towards areas of high EF survival, although local moose populations and movements must be taken into account (see later sections).

Preoviposition period

Several authors (Snowball, 1957; Wilkinson and Wilson, 1959; Patrick and Hair, 1975) have proposed that the preoviposition period of EF ticks is temperature dependent. All have concluded that lower soil and/or air temperatures result in lengthened preoviposition periods. Such was apparently not the case at EINP in 1982 and 1983 because, although the winter of 1981-82 was severe with cold temperatures and deep snow well into April and the winter in 1982-83 was mild (see Appendix 2 and 3), the mean onset of oviposition was similar (7 June, 1982 and 5 June, 1983) (Fig. 20). This suggests the use of a more constant cueing mechanism than temperature.

There is probably a minimum temperature needed to facilitate reproduction, and the probability of reaching this temperature increases as spring advances. However, given the variability found in spring temperatures and the short frost-free period in central Alberta, a more constant and/or precise cue than temperature is needed to initiate oviposition at a time that is likely to optimize successful reproduction. That cue may be photoperiod, with the synchrony of oviposition resulting from some type of facultative diapause of the EF that is terminated by a particular photoperiod. Therefore, the closer the date of EF drop-off is to the critical photoperiod, the shorter the preoviposition period becomes.

Photoperiod affects the initiation and cessation of many insect and vertebrate activities including hibernation, breeding, and molting (Uravov, 1931; Lees, 1955; Beck, 1963; Wigglesworth, 1972). Its relation to the initiation of oviposition in ticks under field conditions has not been studied, although some work on the relation of photoperiod to the rate of oviposition has been done under laboratory conditions (see review of Belozerov, 1982). Belozerov (1982) discussed diapause in ticks and includes the delay of oviposition by EF as a type of morphogenetic diapause. However, little information is given as to whether he is referring to a seasonal diapause leading to synchrony of egg laying as seen

in this study, or to a simple delay in oviposition due to unsuitable conditions at the time EF drop from the host. Balashov (1972) concluded that photoperiod is responsible for the induction of ovipositional diapause in some species of *Ixodes, Haemaphysalis*, and *Dermacentor*, but gives no information on the stimuli that terminate diapause and initiate oviposition. Razumova (1966) and Balashov (1972) proposed a summer diapause in EF *D. pictus* (a three-host tick) as a reliable biological adaptation for prevention of late summer and fall appearance of immature stages that are incapable of over-wintering. The onset of this diapause is thought to be the photoperiod experienced by unfed females (Balashov, 1972). A similar phenomenon with a winter diapause has been reported for EF *Argas arboreus* (Khalili, 1974).

Several other possible cues for the initiation of oviposition exist, including soil temperature and degree days and/or degree hours over a specified threshold temperature. Soil temperatures were not measured in this study, but recordings from a forested site and a bog in Minnesota showed both sites to have congruent warming patterns in soil and air temperatures in spring, although the degree of warming varied annually (Rossman, unpub). If a similar relationship between soil and air temperatures occurred in the three habitats in EINP, as well as the annual variation, soil temperature would not likely provide a suitable constant cue for the initiation of oviposition.

Degree hour summations also do not appear related to the initiation of oviposition. Summations of hours per day with temperatures over 15°C for EF put into the cages at EINP in early April were almost two times greater than those for EF put out in late May (Table 10). It is possible that a certain number of degree hours within a short time span provides a suitable cue for oviposition, but there was no apparent similarity in degree summations for any time between 1982 and 1983 that might result in synchronous oviposition. If a minimum of about 100 degree hours over 15°C is required to initiate oviposition, it is not clear why summation totals of greater than 200 degree hours apparently have no stimulatory effect on the onset of oviposition (Table 10).

Due to annual variations in spring temperatures and subsequent variation in temperature stimulated cueing mechanisms, photoperiod seems to be an ideal cue for the initiation of egg laying by winter ticks in Alberta. However, more research, both under laboratory and field conditions, is needed to prove this and to understand the significance

Table 10. Relationship between degree hours over 15°C and the preoviposition and incubation periods of eng (EF) _Dermacentor_ _albipictus_ in three habitat typ Island National Park, Alberta, 1982.

Date Expt. Started	Bog		Aspen		Grassland	
	Date[a]	Degree Hours	Date	Degree Hours	Date	Degree Hours
PREOVIPOSITION						
March 14	9 Jun	---[b]	---	---	---	---
March 27	8 Jun	---	11 Jun	---	---	---
April 10	9 Jun	272	8 Jun	260	9 Jun	229
April 24	8 Jun	254	7 Jun	244	1 Jun	189
May 8	6 Jun	2	3 Jun	192	9 Jun	194
May 22	6 Jun	1	10 Jun	122	9 Jun	100
Mean	8 Jun	208	8 June	205	6 Jun	178
INCUBATION						
March 14	6 Sep	791	---	---	---	---
March 27	12 Oct	839	11 Oct	719	---	---
April 10	20 Aug	720	27 Sep	739	3 Sep	604
April 24	26 Aug	754	7 Sep	670	16 Aug	588
May 8	22 Aug	740	27 Sep	753	27 Aug	584
May 22	30 Aug	767	3 Sep	622	26 Aug	584
Mean	29 Aug	770	22 Sep	701	25 Aug	590

[a] Average date of either preoviposition or incubation for all that survived and laid viable eggs in each drop period.

[b] Degree hour summations not calculated because weather recording equipment not operable before 1 April.

of this relationship to tick outbreaks.

Incubation period

Even though the preovipostion period appeared to be initiated by photoperiod, the incubation period in the present study was dependent on temperature under field conditions. Differences in incubation period between habitats was apparently due to the presence or absence of a canopy strata which would influence ground temperatures. The dense shade caused by the canopy layer in the aspen habitat resulted in cooler temperatures throughout the summer (Fig. 7) and, in turn, a longer incubation period than in the bog or grassland (Table 7). Other studies have also shown the incubation period for several tick species to be somewhat temperature dependent under field conditions (Hixson, 1940; Snowball, 1957; Patrick and Hair; 1975).

Degree hour summations are probably the most accurate means of expressing the length of the incubation period under field conditions. Approximately 100-150 more degree hours over 15°C were required for hatching in the bog and aspen, than in the grassland (Table 10). The large degree hour summation in the bog was probably due to the wide fluctuations in minimum and maximum temperatures in summer (Fig. 7) which caused repeated interruption of egg development (Table 7). Degree hour summations in the aspen habitat were similar to the bog because of lower minimum temperatures in the aspen (Fig. 7 and 8). The lower summation in the grassland was attributed to higher temperatures that occurred for shorter periods of time than in the bog or aspen (Table 2). Additional study and refinement of these degree hour summations is needed to clarify the relationship between these two variables and to determine if degree hour summations may be of value in predicting reproductive success and hatching dates under field conditions.

Development of eggs during the incubation period was probably delayed by the fluctuating temperature conditions in the field. In order to successfully reproduce, the minimum threshold temperature of development for *D. albipictus* must either be lower than the   °C threshold proposed by Glines (1983), or egg laying and development occurs in short bursts during peaks in maximum temperature. Summaries of monthly weather data for central Alberta from 1970-1983 (Table 11) indicate that mean monthly temperatures below 15°C are common during the summer (June-August). In the present study, EF were subjected to gradually increasing temperatures for early March to late

Table 11. Weather summaries from the Edmonton International Airport, Alberta, 1970-1983.

Month		1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983	30 Year Summary
Mar	T	-8.5	-8.9	-6.1	0.0	-9.4	-9.4	-6.1	-2.8	-3.6	-1.7	-7.2	0.1	-8.6	-4.4	-6.7
	P	2.6	2.1	3.1	1.1	4.0	1.6	1.6	6.7	5.2	8.3	19.5	11.8	32.1	19.3	16.0
Apr	T	3.1	3.3	2.8	3.9	5.0	-1.1	6.1	6.9	4.7	0.8	8.0	4.3	-0.6	4.8	3.2
	P	0.8	0.2	3.9	4.6	1.5	3.0	1.2	18.9	16.1	31.2	4.0	9.7	16.4	18.3	20.2
May	T	10.3	12.2	11.1	12.8	9.4	9.4	11.1	10.4	9.8	8.1	11.3	11.2	10.0	9.9	10.1
	P	2.3	1.3	5.0	3.7	4.0	4.0	3.0	131.9	64.2	86.4	43.0	46.9	27.9	10.2	42.2
Jun	T	16.8	13.8	14.4	15.5	16.6	12.7	12.2	14.2	15.3	14.0	14.5	12.4	15.2	13.6	14.1
	P	8.8	7.6	10.6	14.8	11.7	8.6	9.1	12.5	40.6	70.3	131.9	42.9	25.1	151.1	76.6
Jul	T	16.5	15.0	13.3	17.2	17.2	17.2	15.6	14.2	16.4	16.6	15.5	15.7	16.1	16.6	15.8
	P	12.8	12.7	8.8	8.8	8.8	3.4	7.5	90.7	63.6	111.0	69.2	157.6	204.6	104.5	91.6
Aug	T	15.3	18.0	16.7	16.1	15.0	12.2	16.1	11.7	14.1	15.0	12.5	18.0	13.0	16.8	14.8
	P	2.5	1.0	9.5	11.1	4.9	----	11.1	86.5	111.4	40.9	194.8	10.5	43.2	12.2	78.2
Sep	T	10.8	8.9	5.6	11.1	10.0	10.6	12.2	9.3	9.9	11.9	9.0	12.1	10.7	8.4	9.8
	P	3.4	4.0	4.8	3.4	3.1	----	4.3	38.0	141.5	50.2	55.6	33.4	35.6	36.2	45.7
Oct	T	2.3	3.3	2.8	5.0	8.3	3.3	3.9	4.7	6.5	6.1	5.9	4.1	4.6	4.6	4.7
	P	4.3	0.5	1.1	3.4	0.4	----	1.0	0.4	17.3	12.7	11.2	30.0	39.1	12.2	15.4
Snowmelt		26 Ap	22 Ap	24 Ap	30 Ap	25 Ap	23 Ap	9 Ap	3 Ap	18 Ap	23 Ap	13 Ap	24 Ma	24 Ap	14 Ap	20 Ap
Snowfall		6 Oc	14 Oc	29 Oc	25 Oc	19 No	26 Oc	22 No	17 No	4 No	30 Oc	26 Oc	20 Oc	18 Oc	10 Oc	20 Oc
Total Snow		----	78.8	74.0	54.9	93.0	38.3	43.0	82.4	79.9	125.1	120.0	86.6	171.6	92.0	137.9

T- mean monthly temperature (°C).
P- mean monthly precipitation (mm) calculated as the sum of rainfall plus the water equivalent of snowfall.
Total snow measured in cm.

June, 1982 and 1983 (Appendix 2 and 3). The maximum temperature did not reach 15ºC until mid-April, 1982 a: :· ·/ May, 1983 (Appendix 3). Only EF in the grassland experienced mean ·emperatures above 14ºC and then only for the month of July (Table 12). Nonetheless, EF laid eggs and these eggs hatched in spite of these low temperatures implying that a very low threshold temperature for development is needed to account for the reproductive success of winter ticks under field conditions in central Alberta. If the annual temperature trends shown in Appendix 2 are typical, the proposal of short bursts in egg production and development over a long period is probably the better of the two explanations for the long incubation period in the field. In addition, the long period required from drop-off to egg hatching under field conditions (120-150 days) and the short snow-free period (100-120 days) in central Alberta indicate that *D. albipictus* in central Alberta is close to the northern limits of its range, confirming Wilkinson's (1967) limit of 60º latitude.

Most attempts to extrapolate laboratory-derived reproductive data of ticks to field conditions are probably unjustified because constant temperature and / or relative humidity conditions do not occur in field situation. In this regard, recent literature providing general information on *D. albipictus* in North America (Anderson, 1962; Drummond, 1967; Anderson and Lankester, 1974; and others) contains statements about a summer hatch and delayed larval activation until autumn. As far as can be determined, these statements are the results of erroneous extrapolations from laboratory studies of Hooker (1909), Bishopp and Wood (1913), Howell (1939), and other early workers.

Using field data from this study, a well defined sequence of events from EF drop-off to larval activation can be shown. Assuming 1 April as the peak of EF drop-off (Fig. 15) and that 120-150 days are required from oviposition to egg hatching (Table 7), larvae should be available for transmission to moose in early September. Larvae were not collected by flagging until about 10 September (Fig. 9), indicating that an autumn (Aug-Sept) hatch and a short larval inactivity period occurs, at least in Alberta. Therefore, if one is seeking to predict population trends of ticks, reproductive data should be based on field observations, not extrapolations from laboratory studies under constant conditions.

Table 12. Monthly temperature summaries in three habitat types in Elk Island National Park, Alberta, 1981 and 1982.

Month		1981 Bog	Aspen	Grassland	1982 Bog	Aspen	Grassland
Apr	Max	--	--	--	8.5°C	7.4°C	8.0°C
	Min	--	--	--	-2.5	-3.5	-2.2
	Mean	--	--	--	3.0	1.7	3.2
May	Max	--	--	--	22.1	17.0	18.1
	Min	--	--	--	1.9	3.7	2.4
	Mean	--	--	--	11.8	10.4	10.4
Jun	Max	--	--	--	22.1	20.1	22.7
	Min	--	--	--	4.6	8.4	6.0
	Mean	--	--	--	12.9	14.3	14.4
Jul	Max	21.6°C	19.9°C	--	21.1	18.3	20.8
	Min	9.9	10.8	--	7.9	10.6	9.7
	Mean	15.7	14.9	--	14.5	14.6	15.2
Aug	Max	25.9	22.4	23.4°C	18.3	15.6	16.6
	Min	7.8	10.6	7.0	5.4	7.5	6.8
	Mean	16.8	16.5	15.3	11.8	11.6	11.8
Sep	Max	19.0	17.2	18.0	17.4	14.7	14.6
	Min	2.8	5.9	1.8	2.0	5.0	1.9
	Mean	11.1	11.5	9.9	9.1	9.9	8.7
Oct	Max	9.3	9.3	7.4	11.2	11.0	9.3
	Min	-2.1	-0.8	-3.0	-3.2	0.3	-5.6
	Mean	3.7	4.1	2.5	4.0	6.2	1.9
Nov	Max	3.4	3.8	5.5	-1.8	-4.0	-6.1
	Min	-6.5	-3.2	-4.5	-10.5	-10.6	-14.8
	Mean	-1.6	0.4	0.8	-5.6	-7.3	-10.4
Dec	Max	-4.1	-3.7	1.3	-5.8	-5.3	-10.1
	Min	-15.3	-11.4	-10.3	-10.0	-12.8	-19.5
	Mean	-9.7	-7.6	-4.6	-10.0	-9.1	-15.1

Patrick and Hair (1975) obtained reproductive data for *D. albipictus* under field conditions in Oklahoma, which is in a prairie biome and is climatically distinct from Alberta. If 12°C and 4 cm precipitation are arbitrarily assumed to be the lower threshold of development, the entire reproductive period, with the exception of larval activation occurs during the months that fall above the proposed minimum (June, July, and August) in both Oklahoma (Fig. 21), and Alberta (Fig. 22). Although these minimum criteria are highly subjective, they do provide a common pattern for development of winter ticks in two climatically distinct areas and may be useful to determine the actual range of *D. albipictus* and identify areas suitable for reproduction where winter ticks are currently not found such as Alaska.

C. Reproduction of engorged females under laboratory conditions

Constant conditions

Because most arthropod reproductive studies are done under constant laboratory conditions, the data and discussion in this section provide some comparative information for EF *D. albipictus* under constant, cold stress, and fluctuating conditions. As far as can be determined, the current study is the only reproductive study that utilized multiple replicates along a time series within the treatment groups. The following discussion also provides some information on aspects of the transmission of winter ticks to moose.

A review of the reproductive performance of *D. albipictus* under constant laboratory conditions confirms that EF in this study were basically similar to EF incubated at similar temperatures from other regions of its range in North America (Table 13). Some or all of the variation in Table 13 could be explained by differences in methodology including the weighing of eggs instead of total egg counts, use of different host animals, different photophase during incubation, time of year EF were collected, and differences in EF size.

Engorged female weight

Weights of EF in this study were similar to EF in other studies on *D. albipictus* (Table 13), although EF from moose are usually heavier than those from bovine hosts. Differences in weight could also be attributed to date of collection, and regional differences in tick size, although the effect of differences in weight on reproductive

Figure 21. Climograph for Cookson Hills State Wildlife Area,

Oklahoma, 1975. (Data provided by A. Kocan, Oklahoma

State University, Stillwater, OK)
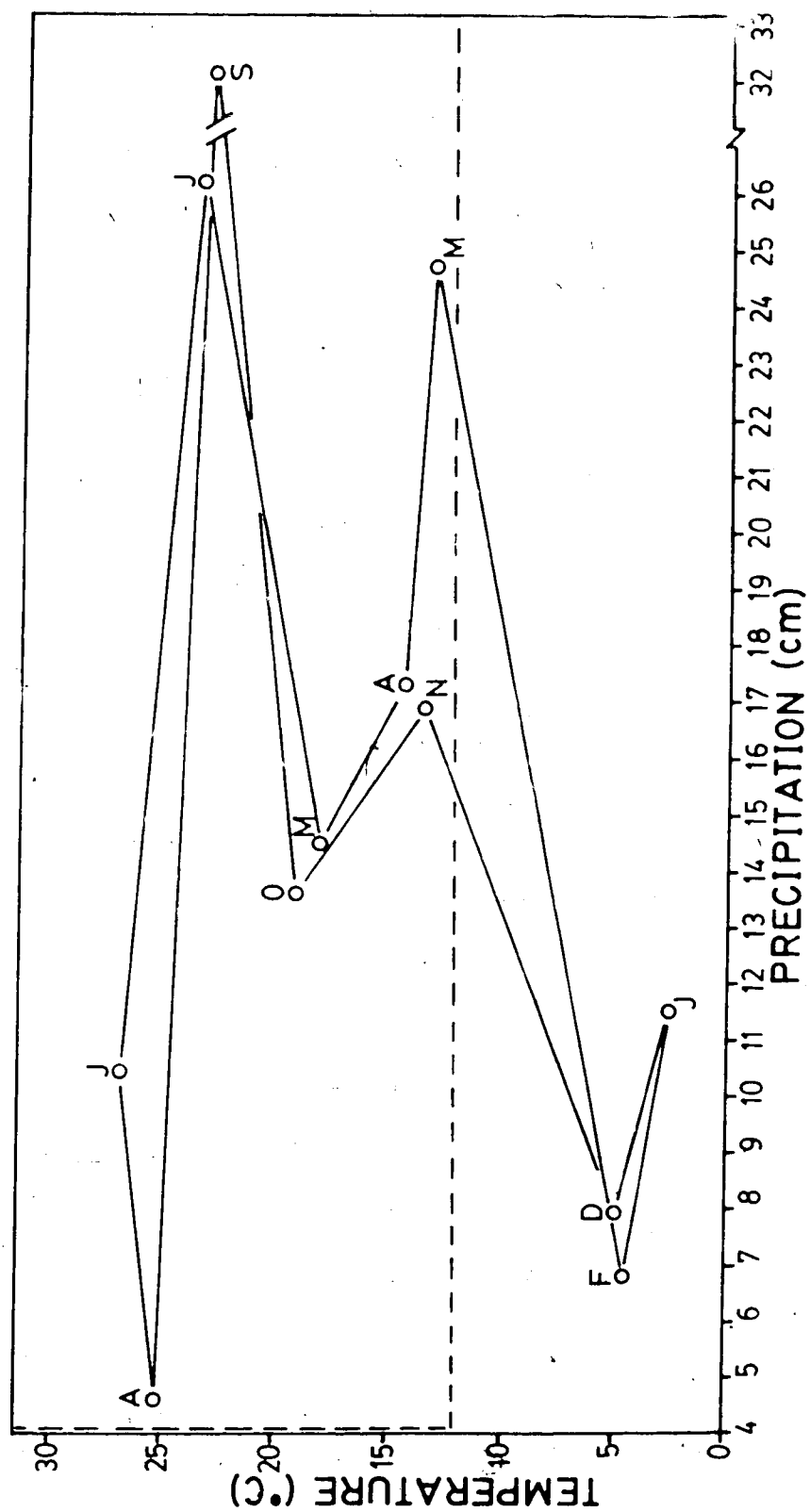
Figure 22. Climograph for Elk Island National Park, Alberta, 1981-83 (O)

'and Edmonton International Airport, 1940 - 1981 (●).

Table 13. Reproductive parameters of engorged female (EF) *Dermacentor albipictus* under laboratory conditions: a review.

Host[a]	Conditions	n	EF Weight (g ± SD)	Preoviposition (days ± SD)	Incubation (days ± SD)	Total Production (eggs/EF ± SD)	Reproductive Efficiency Index (REI) (eggs/gEF)	Source
--	10°C 80%RH[b]	3	--	3-48	--	--	--	Wilkinson, 1967
--	15°C 80%RH	3	--	6-34	151	--	--	Wilkinson, 1967
--	15°C 60-100%RH	9	--	--	--	--	--	Howell, 1939
--	18-20°C moist sand	2	--	--	67.0	--	--	Bishopp & Wood, 1913
M	19°C 85%RH 12:12	20	0.589 ± 0.149	21.3 ± 4.9	48.5 ± 3.5	4754 ± 1015	8071	Glines, 1983
M	19°C 85%RH 12:12	136	0.536 ± 0.167	21.5 ± 4.7	--	--	--	Present study
--	20°C 80%RH	3	--	6.8	57-62	--	--	Wilkinson, 1967
--	20°C 60-100%RH	9	--	--	57.2	--	--	Howell, 1939
--	20-21°C moist sand	1	--	--	58	--	--	Bishopp & Wood, 1913
--	21-22°C moist sand	3	--	--	52.3	--	--	Bishopp & Wood, 1913
--	22°C 70-80%RH dark	252	0.47 ± 0.12	11.1	47.9 ± 2.9	4147 ± 2108	8823	Addison & Smith, 1981
--	22-23°C moist sand	4	--	--	50.8	--	--	Bishopp & Wood, 1913
--	23-24°C moist sand	2	--	--	49.5	--	--	Bishopp & Wood, 1913
--	24-25°C moist sand	4	--	--	42.0	--	--	Bishopp & Wood, 1913
M	25°C 85%RH 12:12	19	0.610 ± 0.136	8.7 ± 2.1	41.5 ± 1.6	4149 ± 1143	6801	Glines, 1983
--	25°C 80%RH	3	--	2-3	34-39	--	--	Wilkinson, 1967
--	25°C 60-100%RH	9	--	--	35.8	--	--	Howell, 1939
M	25°C 85%RH dark	91	0.470 ± 0.236	8.3 ± 3.6	36.8 ± 4.8	3731 ± 2146	7940	Present study
--	25-26°C moist sand	2	--	--	38.5	--	--	Bishopp & Wood, 1913
M	26°C 30-50%RH dark	51	0.39 ± 0.17	10.2	31.5 ± 1.0	2707 ± 1323	6941	Addison & Smith, 1981
M	26.7°C 85%RH	25	--	--	28.2 ± 0.5	3835	--	Howell, 1939
B	26.7°C 80%RH	20	0.156	6.3	--			Ernst & Gladney, 1975

Table 13. (Continued).

host	Conditions	n	EF Weight	Preoviposition	Incubation	Total Production	REI	Source
--	26-27°C moist sand	3	--	--	39.3	--	--	Bishopp & Wood, 1913
H	27°C 70-90%RH dark	23	0.420	11.8	25.7	3864	9200	Drummond et al. 1969a
H	27°C 80%RH 12:12	--	0.431	10.8	26.0	3771	8749	Wright, 1971
B	27°C 80%RH various	--	--	--	33.5	--	--	Wright, 1969a
--	27-28°C moist sand		--	--	33	--	--	Bishopp & Wood, 1913
M	30°C 80%RH dark	2	0.626 ± 0.112	5.6 ± 1.3	24.3 ± 1.9	3626 ± 1133	5792	Glines, 1983
--	30°C 80%RH	3	--	2-3	27-29	--	--	Wilkinson, 1967
--	30°C 6-90%RH	9	--	--	29.1	--	--	Howell, 1939
--	32.2°C moist sand	3	--	17.6 ± 0.41	--	1873 ± 397	--	Bishopp & Wood, 1913
--	35°C 80%RH	3	--	2-3	27-39	--	--	Wilkinson, 1967
--	35°C 8%RH	9	--	2-3	27-39	--	--	Wilkinson, 1967
--	35°C 90-100%RH	9	--	--	22	--	--	Howell, 1939

[a] B - Bovine, H - Horse, M - Moose

[b] RH - Relative Humidity

[c] photophase

potential expressed as REI is unknown (Table 13).

The results of this study show clearly that a decrease in weight of EF occurs over time (Fig. 17). Weights of EF used in these reproductive studies were similar for all successive drop periods due to random selection of EF. If selection of EF had not been random or all EF used in one treatment, the decrease in weight would probably have been reflected in lower reproductive parameters with successive drop periods. This decreased productivity by lighter EF that are dropped in late winter may have important implications in the dynamics of tick transmission under field conditions and for comparative studies on reproductive potential of EF under laboratory conditions.

Preoviposition period

The preoviposition period is dependent, to some degree, on temperature under constant conditions (Table 13); being shorter at higher temperatures. Because incubation conditions of EF in this study were the same for each experimental replicate within a treatment group, it was assumed that all reproductive parameters would be constant. Given this, the declining preoviposition period for EF of successive drop periods in all treatments (Fig. 19) in this study was completely unexpected and has not been reported previously. The change in preoviposition period was not related to EF weight or incubation conditions.

One possible explanation for this observation is that, because the EF were collected from moose housed outdoors, they were exposed to a certain photophase for a short period prior to collection. Thus, a photoperiod-induced, biological rhythm is proposed for regulation of the onset of oviposition. The initial starting point of this rhythm is speculated as the photophase experienced by the EF at the time of drop-off. In the absence of further photoperiodic cues, the initial cueing mechanism seems to exert a greater influence than temperature on the onset of oviposition, although temperature may regulate the preovipositional maturation process of the reproductive tract of EF. The closer the photoperiod experienced by the EF is to the critical photophase that stimulates the initiation of oviposition, the faster the clock mechanism moves (Table 14). The interactions between photoperiod and temperature as a possible cueing mechanism cannot be overlooked, but the interactive mechanism is unknown. There is a need for similar studies to be conducted on both winter ticks and other tick species to determine is this

Table 14. Relationship between daylength at date of collection and the preoviposition period of engorged female <u>Dermacentor</u> <u>albipictus</u> under constant 25°C, 1982.

Date out	n	Day Length[a]	Preoviposition period (Days ± 1 SD)
March 17	3	11 hr 56 min	9.0 ± 3.5
March 27	20	12 hr 39 min	11.0 ± 3.0
April 11	15	13 hr 42 min	8.3 ± 1.7
April 24	23	14 hr 36 min	7.7 ± 2.9
May 8	13	15 hr 29 min	6.4 ± 2.9
May 22	10	16 hr 15 min	4.0 ± 1.7
June 5		16 hr 48 min	

[a] Time from sunup to sundown.

declining preoviposition period is characteristic of ticks in general or is restricted to species in northern latitudes.

Incubation period

The incubation period of *D. albipictus* is inversely related to temperature under constant conditions (Table 13). A similar relationship has been shown for many other tick species (Czapska, 1967; Sweatman, 1967; Bennett, 1974; Campbell and Glines, 1979; Campbell and Harris, 1979; Koch and Dunn, 1980; and others). Temperature appears to affect the metabolic rate of the developing larvae and increases the velocity of development with increasing temperatures until an upper critical limit is reached. Because temperature was constant between replicates within a treatment group, no change occurred in the incubation period of EF in successive drop periods within treatment groups studied suggesting that incubation is a temperture dependent parameter.

Other parameters

In all experimental treatments in the laboratory, the total number of eggs produced was significantly positivley correlated with EF weight. This relationship has been established in numerous other studies on tick reproduction (Snow and Arthur, 1966; Sweatman, 1967; Sonenshine and Tigner, 1969; Drummond et al. 1969a, 1969b; 1971; Koch and Dunn, 1980; Davey et al. 1980a and 1980b; Koch, 1982; and others).

The REI calculated in Table 13 may be an underestimation of the reproductive efficiency found in some studies because it was calculated using average EF weight and average number of eggs per EF from literature sources. However, it serves as a useful comparision between reproductive studies under a wide range of experimental conditions. There may be a difference in REI between EF from different parts of the range of winter ticks, however, more work at different temperatures in the southern part of the range of *D. albipictus* is needed to clarify this relationship.

Cold stress conditions

Various temperature regimens were utilized in an attempt to explain some of the differences between the results of the experiments at constant temperatures and field conditions in the present study. Although these experiments were not designed to simulate field conditions, the temperature regimens were chosen to approximate a temperature or temperature range that EF would be exposed to under field conditions in

central Alberta. As far as can be determined, little work of this nature has been done on other species of ticks and it is suggested that further study is needed to determine if these findings are important to the reproductive success of ticks.

Although most reproductive parameters were reasonably similar for most experimental replicates within each treatment group, the preoviposition period declined with successive replicates in all treatments as was shown for the constant temperature and field condition treatment groups (Fig. 19 and Tables 5 and 6). The declining preoviposition period was assumed to be due to the photoperiod to which the EF was exposed prior to collection as explained earlier. The effect of photoperiod on the preoviposition period of EF stressed at field conditions in EINP cannot be overlooked as a partial explanation for the shorter preoviposition period observed.

Unlike the preoviposition period, the length of the incubation period did not change when EF *D. albipictus* were cold stressed indicating either that ovarian development and maturation can occur at sub-optimal temperatures for oviposition or that development and maturation of eggs at constant 25°C is not affected by prior cold stress to the EF. If the lower limit of development and reproduction is around 15°C, the metabolic rate of EF at temperatures of 10°C or less is probably too low to allow growth and development of body organs so the latter explanation is more likely.

The most startling finding in this part of the study was that cold stress of EF followed by incubation at constant 25°C increased the reproductive potential by somehow increasing the efficiency of egg production and allowing more eggs and more eggs per gram EF to be produced. The mechanism that allows the increased efficiency is unknown, but is thought to be due to some physiological change that alters or reroutes energy allocation of various body processes, or a lowered energy of maintenance due to the cold stress. The cold stress also increased the survival potential of larvae, although the mechanism by which this occurs is also unknown. Little information is available on increasing reproductive output or efficiency of arthropods in response to cold stress.

Fluctuating conditions

Survival and reproduction of EF *D. albipictus* under fluctuating conditions was less than that found at constant 25°C, implying that these temperature regimens were sub-optimal. Reproductive parameters of EF under fluctuating conditions were most

similar to those under field conditions and may have been limited by the experimental conditions and equipment malfunctions that resulted in very low relative humidity at times in three of the five fluctuating treatment groups.

The production of eggs by EF subjected to fluctuating conditions was not surprising based on the successful reproduction under similar fluctuating conditions in EINP. Although only a small percent of the eggs laid actually hatched, the fact that the eggs could develop when repeatedly subjected to freezing temperatures, was surprising. The eggs must contain a cryoprotectant that is either produced by the reproductive tract of the EF or by the developing larvae.

The long periods of preoviposition and incubation under fluctuating conditions in the laboratory support the short burst view of egg production and development seen under field conditions. This could explain the doubling in time required for reproduction in the long cold, short warm treatments over the reverse treatments (Table 8). The small sample size of successful EF did not allow a more detailed comparison between treatment groups.

The fact that total production and REI were similar for EF under fluctuating conditions and at constant 25°C suggests that the fluctuating temperature regimens in this study were not detrimental to the maturation and development of the EF reproductive tract. The continual interruption of egg laying did not seem to affect the efficiency of reproduction. Similar results were obtained with EF *A. nitens* incubated at 12 hours 27°C, 12 hours 16°C and a 12:12 photophase (Wright, 1969a).

Fluctuating temperature can either retard, accelerate, or have no effect on development of insect eggs (see review of Bursell, 1974). The differences can usually be attributed to differences in the point in the thermal developmental range about which the fluctuation in temperature occurs. The thermal developmental range of winter ticks appears to be from about 19°C to 30°C (Table 13). In the present study, repeated exposure to suboptimal temperatures appeared to cause a retardation of development.

Due to the complex interactions that occur when comparing the reproductive timing and potential of EF under different treatment regimens, one is forced to conclude that EF *D. albipictus* have wide tolerance limits of temperature and relative humidity for successful reproduction. These experiments also point out that reproductive

experiments carried out under constant conditions may lead to erroneous conclusions wh.. applied to field situations. Further refinement of the periodicity of the temperature fluctu..ion is necessary before laboratory simulation of reproduction under field conditions can be used in attempts to apply these findings to field situations.

D. Movements and activity of larval ticks

In the present study, eggs of *D. albipictus* hatched from mid-August to late September and larvae began ascending the vegetation about two weeks later (pers. observ.). Most literature sources refer to a summer hatch and a delay in host seeking by winter tick larvae until early autumn. This delay between hatching and ascension of vegetation by larvae has been referred to as a resting period (Bishopp and Wood, 1913), dormancy (Cameron and Fulton, 1926-27), an inactive state (Howell, 1939), quiescence (Drummond, 1967), and diapause (Wright, 1969b).

The definitions of these terms in the literature are unclear. Diapause usually refers to a period of suspended or arrested development that is caused by a lack of or low production of hormones necessary for growth and is not immediately referrable to prevailing environmental conditions (Wigglesworth, 1970, 1972; Belozerov, 1982; Chapman, 1982). Diapause is commonly divided into three types depending on the induction and termination mechanism (Wigglesworth, 1970; Chapman, 1982; Saunders, 1982). Obligatory diapause (porapause) is genetically determined to occur at a particular stage in the life cycle and is independent of environmental conditions. Facultative diapause (eudiapause) is a facultative cessation of development induced by one stimulus, such as photoperiod, and terminated by another, such as chilling. Oligopause is a facultative arrest of development induced and terminated by the same stimulus, usually photoperiod.

Diapause is thought to be an adaptive phenomonen to synchronize development with periods of favorable conditions (Belozerov, 1982; Chapman, 1982), and to allow synchronization of the life histories of the sexes (Hemming, per comm). In ticks, it is commonly expressed as either a behavioral diapause as in the delay of host seeking behavior and/or engorgement or a morphogenetic diapause as in a delay in morphogenesis and/or reproduction (Belozerov, 1982).

Other terms that have even more ambiguous definitions are often used interchangeably with diapause. Dormancy usually refers to inactivity with a low metabolic state. Estivation refers to dormancy during summer or a dry period while hibernation refers to dormancy during the winter. Quiescence is a state of inactivity, dormancy, or delayed development that is referable to immediate environmental conditions. It is often included as a form of diapause or dormancy, but has not been shown to be due to the lack of a growth hormone (Wigglesworth, 1972; Chapman, 1982; Saunders, 1982). Due to the ambiguous definitions of these terms and the incomplete knowledge of the nature of arthropod inactivity, these terms should be used only with great caution.

The period of inactivity of larval winter ticks from hatching to ascension of vegetation in autumn should probably be referred to as quiescence as it has not been shown to be due to the lack of a growth hormone, and appears related to local weather factors. The possibility of a genetically determined diapause must not be excluded. The quiescent period of larvae under field conditions aries g eat / with geographical location: four to seven months in California (Howell, 1939), four to five months in Oklahoma (Patrick and Hair, 1975), three to six months in Texas (Bishopp and Wood, 1913), two to three months in British Columbia (Wilkinson, 1967), and about two weeks in Alberta (present study).

The activation of winter tick larvae after the quiescent period has been attributed to the advent of frost in autumn (Cowan, 1946), a complex interaction between photoperiod and above freezing soil temperatures (Wilkinson, 1967), and photoperiod alone (Wright, 1969b and 1971). Wright (1969c) was able to terminate 'diapause' in larval *D. albipictus* by immersing them in an analog of molting hormone or alpha-ecdysone. However, a specific incident or change in temperature or relative humidity common to both years in this study that might initiate larval activity was not apparent, although a day to day comparison of weather and larval activity was not possible. A response to photoperiod seems to be the most plausible explanation for the constancy in the initiation of larval activity (early September) in both years of this study. Wright (1969b and 1971) induced diapause of larval winter ticks by long photophases and cessation of diapause by short photophases similar to what they would be exposed to under field conditions in autumn.

Photoperiod may partially explain the similarities between the onset of larval activity (September to early October) in Alberta (present study) and British Columbia (Wilkinson, 1967) which are in close geographic proximity. Depending on the photoperiod during mid-November in Oklahoma, this hypothesis may also explain the differences in the ascension dates of larvae found by Patrick and Hair (1975) and the present study. If photoperiod is an important cue for larval activation, the differences in onset of larval activity may be due to differences in the 'message' received by the larvae (Holmes, per comm). The 'message' could require immediate activation in the north (Alberta) and set off a timing mechanism to induce activation at a later date in the south (Oklahoma). Further work is needed regarding the cause of the initiation of larval activity under field conditions, as well on the mechanism by which photoperiod might cue larval activation.

Almost all larvae were in clumps at the tips of the vegetation and, thus, were available for transmission to moose continously from September to November except for periods of cold temperatures. Due to the overbrowsed condition of the vegetation in EINP, most larval clumps were about one to one and a half m above the ground. This is probably an optimum height for host acquisition, being approximately chest high on a moose or wapiti. Wilkinson et al. (1982) found larval *D. albipictus* in EINP, but did not quantify distribution or height preference.

The reason larval ticks clumped on vegetation is unknown. It is almost certainly an active and/or selective process because random choice of vegetation, especially of individual branches on a single plant, would result in wide dispersal of larvae. The clumping behavior displayed by larvae may be due to an aggregation substance, possibly a pheromone (Sonenshine et al. 1982).

The clumping behavior may have several adaptive advantages including protection from desiccation and enhancement of host acquisition. The over-dispersed or clumped distribution of larvae may ensure that as a host passed by, more larvae would be able to attach. While the probability of a moose encountering a clump of larvae may be low, once a clump is touched, a large number of larvae could attach at one time. If 'ticky' moose use similar areas regularly throughout the year, especially in late winter and autum probability of encountering larval clumps in these areas in autumn would be inc.

Therefore, having larval clumps at optimum heights in optimal locations for transmission should enhance host acquisition.

Other studies with ticks and other ectoparasites have shown that parasites concentrate either on or off the host presumably to facilitate host transfer or host acquisition. Parish (1949) found large concentrations of *Otobius megnini* around cattle salt troughs in Texas, but the concentrations may have been due to the large amount of time spent by cattle at the troughs rather than to directed movements by ticks. Gregson (1951) reported concentrations of *D. andersoni* along the edges of game trails in spring. Large concentrations of clumps of *B. microplus* larvae occur in bedding sites of cattle (Wilkinson, 1953 and 1961). Fleas (*Spilopsyllus cuniculi*) congregate on the head of pregnant rabbits and transfer to the young when the female cleans them after birth (Rothschild, 1965). Samuel and Trainer (1971) reported a higher concentration of lice in the groin area of white-tailed deer during autumn, presumably to facilitate transfer during breeding.

The observation that larval *D. albipictus* do not exhibit a diurnal, vertical migration presents an apparent paradox between success of transmission and desiccation, which is difficult to explain. Although many tick species exhibit clumping behavior to facilitate host acquisition (Parish, 1949; Gregson, 1951; Lees and Milne, 1951; Wilkinson, 1953, 1961), some reports indicate a diurnal migration of ticks to replenish body water lost while exposed to dry air at the tips of the vegetation (Lees and Milne, 1951; Camin and Drenner, 1978; Yosida, 1979; Knulle and Rudolph, 1982).

Almost all ticks have some water conserving adaptations, but the extent of development and utilization of these adaptations is dependent on climatic factors in the habitat in which the tick exists (see review of Knulle and Rudolph, 1982). Most tick species can survive desiccation for various lengths of time, although intensive research into water balance mechanisms is relatively recent. It is known that unfed ticks have three major means of regaining body water: migration to the soil duff; uptake of water vapor from the atmosphere; and imbibation of water from dew or rain droplets. It seems that the lack of a diurnal, vertical migration by larval winter ticks may be due to a highly developed water conservation mechanisms, and although speculative, a well developed ability to extract water from the atmosphere when relative humidity levels peak during the

night. Further work is needed to determine the mechanism by which this occurs and to aid in the solution of this question.

Unlike some studies of ticks (McColluch and Lewis, 1968; Lewis, 1970; Rechav, 1979), horizontal dispersal of larvae in the present study appeared minimal. Most larvae seemed to ascend vegetation in the immediate vicinity of the hatching site and the distribution of larvae was assumed to be directly dependent on the distribution of EF. Similar findings have been reported by Lees and Milne (1951) for *I. ricinus* and Bishopp and Hixson (1936) for *A. maculatum*.

There have been few studies of the relationship between ambient temperature and larval tick activity under field conditions. Most poikilothermic animals tend to slow their metabolic rate when temperatures decrease, thus either slowing or stopping movement (Schmidt-Nielsen, 1970). If this principle is applicable to larval winter ticks, the gradual decline in larval numbers flagged in autumn around moose carcasses (Fig. 9) may be explained by the general decline in daily temperatures that occurred during the same time period. The abrupt decline in mid-November from temperatures averaging over 0°C to temperatures averaging below 0°C (Appendix 2) appears to have a cause/effect relationship to the marked decline in larval numbers flagged around carcasses in both 1981 and 1982 (Fig. 9).

The minor increases and decreases in the numbers of larvae flagged around carcasses in both years (Fig. 9) appears related to ambient temperature on the day of sampling. On days of low numbers of larvae flagged, temperatures were either declining or near the low point of a cold period, while high numbers of larvae flagged usually occurred when temperatures were increasing or near the high point of a warm period (Appendix 2 and Fig. 9).

The lack of a definite peak in larval numbers at carcasses in early October, 1982 (Fig. 9) may have also been due to weather conditions. A freezing rain fell on 29 and 30 September and 4 and 5 October, 1982. Minimum temperatures during and immediately after these days dropped to below 0°C and froze many of the larvae to the vegetation they had ascended. These larvae were unavailable to the flagging technique and the peak in numbers could easily have been missed.

D. albipictus probably has only one generation (egg to EF) per year throughout its range. Two important observations in this study support this conclusion: no viable larvae were found on any carcass sites by flagging in spring, and, experimental and free-ranging moose were free of ticks from early June to late August (Samuel, unpub; Glines, 1983; pers. observ.). This is in agreement with other studies on *D. albipictus* in Oklahoma (Patrick and Hair, 1975), British Columbia (Wilkinson, (1967), and Texas (Bishopp and Wood, 1913; Drummond, 1967), but not in California (Howell, 1939).

Howell (1939) found three distinct peaks of larval activity on horses in California which he associated with two generations of ticks per year. He believed the second peak was a result of experimental animals being given access to previously undisturbed pastures and picking up quiescent larvae from the first generation in September. He concluded that the third peak (January) was due to acquisition of larvae that hatched from eggs laid by EF dropped from the initial infestation in September. Unfortunately, the experimental work to support this hypothesis was done under unspecified conditions and does not appear sufficient to justify the conclusion of two generations per year without supporting data from seasonal larval collections in the field.

Flagging techniques are commonly used to estimate tick populations (Wilkinson, 1961, 1967; Semtner et al. 1971b; Campbell and Harris, 1979; Kgoroba, 1979; Barnard, 1981). Flagging may be less effective than CO_2 traps for determining populations of non-adult instars in areas of dense vegetation (see Wilson et al. 1972 and Semtner and Hair, 1975 for explanation), but may be the most effective technique for estimating numbers of ticks available to host animals in local areas. The numbers of larvae flagged at each carcass in autumn was probably related to the date each moose died. The prevailing weather conditions at the time of death would determine the subsequent survival rate of EF present. Date of death would also influence the numbers of EF per moose; more being present in April and May than any other time. The importance of carcass sites to the transmission of winter ticks remains to be investigated.

Preliminary results suggest a potential relationship between numbers of larvae flagged in autumn along trails and tick loads per moose collected the following winter. Tick infestations, as determined by hide digestion for 1981-82, averaged sightly over 80,000 per moose, the highest found since tick monitoring in EINP began in 1978

(Samuel, unpub). In 1981, the mean number of larvae flagged per 20 m trail for the entire sampling period was 43. Assuming constant distribution of larval clumps along game trails, a moose would have had to travel 37.2 km in the three months of larval activity to acquire 80,000 ticks. This distance is easily within the limits of daily moose movements in autumn (Edwards and Ritcey, 1956; Knowlton, 1960; Van Ballenberghe and Peek, 1971).

In 1982-83, tick infestations per moose averaged about 25,000 (Samuel, unpub) and the mean number of larvae flagged per 20 m of trail in the same areas in 1982 was 0.2. Again, assuming constant distribution of larval clumps, a moose would have had to travel 25,000 km to acquire 25,000 ticks. This figure is greatly exaggerated due to the very poor results obtained by trail flagging in 1982 and is unrealistic, but the trend is obvious. It is not known whether the poor flagging results in 1982 were due to changes in moose movements in response to flagging activity along the trails the previous autumn; to extended movements by moose away from these areas during the severe winter of 1981-82; or to low survival of EF in spring, 1982.

Given that moose move an average of slightly over 1 km per day for moose in autumn (Edwards and Ritcey, 1956; Knowlton, 1960; Van Ballenberghe and Peek, 1971), and the long period of larval activity in the present study, it seems reasonable to assume that a short exposure period for moose is unlikely. The continual acquisition of larvae for two to three months during larval activity is more realistic. Although peak exposure appears to be early October, the length of the exposure period appears dependent on temperature declines in autumn. Early frosts and snowfalls act to shorten the exposure period by decreasing activity and increasing mortality of larvae, thus possibly reducing numbers of larvae to which moose would be exposed.

The peak of larval activity in early October corresponds very well with the peak of the moose rutting season (defined as the period of activity and seeking of mates just prior to or during the breeding season) which usually extends from mid-September to mid-October (Peterson, 1955; Dodds, 1958; Lent, 1974). Male moose tend to travel farther than females during the rut (Phillips et al. 1973; Roussel et al. 1975) and as a probable result, average twice as many ticks per individual as females ($\bar{x}$=45,341 and 21,120, n=18 and 24 for males and females, respectively)(Samuel, unpub). Calves average 44,889 ticks per individual (n=29)(Samuel, unpub). possibly due to either

displacement from the cow during the rut and subsequent wandering and increased daily movements, or to a weak immune response to the ticks. This association may be coincidental, but Nelson et al. (1975) confirm that, for unresolved reason(s), males of many host species carry a larger population of ectoparasites than females.

Habitat preference and temporal separation of the rut of the major ungulate hosts of the winter tick may explain why larvae seem to be attuned to moose. Wapiti tend to prefer open, grassy areas and rut in early September (Murie, 1979; Wishart, 1981; pers. observ.), before the major period of larval activity. White-tailed deer are sympatric with moose over much of their range, but rut in late November, after the major period of larval activity. Limited daily movements by wapiti and deer in early October through areas heavily used by moose in late winter may explain the lower numbers of ticks (Samuel, unpub.) found on these two ungulates. Larvae may also have some mechanism for distinguishing between host species and may select moose over other ungulates.

E. Experimental infestations of captive moose

Moose calves experimentally infested with 30,000 *D. albipictus* in this study apparently tolerated the infestation fairly well. They did spend a good proportion of their time grooming (Samuel, unpub; pers. observ.), and as a result, removed much of their winter hair coat prematurely. Specific differences in hair loss, tick movements, and tick density between mass- and trickle-infested moose calves will be discussed elsewhere, but general comments on the results of these infestations are applicable to the transmission of *D. albipictus* in Alberta.

Although anorexic affects and weight loss due to tick infestations of cattle have been reported (O'Kelly and Seifert, 1969; Seebeck et al. 1971; Williams et al. 1978; Corrier et al. 1979), the specific cause of the anorexia has not been established. Anorexia and weight loss due to ticks were not observed in moose calves in the present study. The declining weight changed per week and weight gains per kg of food consumed towards the end of the experiment (Fig. 13) were attributed to a normal growth pattern, not to the presence of ticks. However, occassional declines in weight due to feed changes, pneumonia (MO 68), and other health problems (MO 48,50,55, and 60) were observed.

Most ungulates exhibit seasonal differences in food consumption, usually showing a marked drop in consumption during late fall and winter and increased intakes in spring and summer (Fowler et al. 1967; Ozoga and Verme, 1970; Verme, 1970; Moen, 1973 and 1978). Further study of the health status and food intake of free-ranging moose is needed to determine if winter ticks produce an anorexic affect greater than the normal seasonal variation.

The exposure of calves to larvae over a long period of time (trickle-infested) resulted in a longer duration of larval and engorged larval instars when compared to calves with a short exposure period (mass-infested) (Fig. 14). Synchrony of tick development from engorged nymphs to EF on both infestation groups resulted from the long period of nymphal inactivity. The timing of tick development on trickle-infested moose is closer to the timing of tick development observed on free-ranging moose (Samuel and Barker, 1979; Glines, 1983).

The pattern of development observed appears consistent in most of the northern parts of the range of *D. albipictus* (Cameron and Fulton, 1926-27; Fenstermacher and Jellison, 1933; Lamson, 1941; Cowan, 1946; Addison et al. 1979; Samuel and Barker, 1979; Glines, 1983). In contrast, there is apparently no period of nymphal inactivity of winter ticks in the southern part of its range. There, *D. albipictus* can complete the parasitic phase of its life cycle in as little as 21 days (Drummond et al. 1969a), 30 days (Ernst and Gladney, 1975), and 30-33 days (Howell, 1939) on cattle housed under constant laboratory conditions.

Using the definitions discussed earlier (p. 99), the period of nymphal inactivity in the northern part of the range of *D. albipictus* is probably a form of behavioral diapause. It may be genetically determined to occur at the nymphal stage, but appears to be terminated by a photoperiodic cue. The diapause of nymphal winter ticks probably acts to synchronize the development of EF with more favorable conditions for reproduction in spring as well as synchronizing the timing of appearance of males and females. Other northern one-host (*Hyalomma scupense*) and winter season ticks (*D. pictus*) undergo a seasonal diapause while on the host for similar reasons (Belozerov, 1982).

High tick loads have been associated with hair loss on moose in Alberta (Samuel and Barker, 1979). All infested, captive moose in this study and those of Glines (1983)

lost at least some of their winter hair prematurely, a finding that supports the proposal of Samuel and Barker (1979) that ticks are responsible for the premature loss of winter hair on free-ranging moose in central Alberta.

Despite the two different infestation techniques used in this study, hair loss patterns on calves did not differ greatly, although mass-infested calves began grooming on the thigh (Fig. 18). The trickle-infestation technique was assumed to be a more natural technique and the initial grooming and hair loss along the thigh of mass-infested calves was attributed to a response to the presence of ticks in a 'abnormal' location early in the course of the infestation. There was no apparent relationship between tick density and areas groomed by experimental moose. Hair loss generally started on the side and was attributed to accessibility in response to a generalized irratation. Areas of tick concentration may represent areas of ineffectual grooming attempts by moose or aggregation at preferred developmental sites rather than accelerated development. Since extensive premature loss of winter hair has not been reported on other hosts infested with ticks, there is probably nothing comparable in the literature, although Riek (1956) and Corrier et al. (1979) report hair loss on cattle after infestation with *B. microplus*.

The decline in weight of EF *D. albipictus* during the period of EF drop-off suggests that either engorged nymphs that molt late produce smaller adult females or, possibly, that moose mount some form of immunological response to limit either the amount of blood ingested or the feeding time of females. The immunological response may be expressed as grooming because higher frequencies and longer duration of grooming bouts tend to occur in late winter when females are engorging (Samuel, unpub; pers. observ.). The grooming may interrupt feeding by or dislodge EF before engorgement is complete resulting in lower weights of EF. Similar declines in weight of EF *B. microplus* over time have been reported (Reik, 1962; Bennett, 1969), and have been attributed to grooming and resistance in cattle.

Because total production is directly related to EF weight, the decline in EF weight over time probably causes a reduction in reproductive potential. This weight change could be very important in the epizootiology of winter tick infestations on moose due to the decreasing number of eggs laid by lighter EF dropped near the end of the infestation. Further study of the relationship between EF weight, time of drop-off, and productivity

are needed to clarify the importance of these factors to the transmission of *D. albipictus*.

The reason(s) why a low proportion of the larvae were recovered as EF in this study ($\bar{x}=1.5\%$) are not known, but other workers have reported similar findings (Hunter and Hooker, 1907; Gladney et al. 1973). The extensive grooming (i.e.; chewing, licking, scratching, and rubbing) done by moose in response to ticks would certainly dislodge many ticks. Sensitivity, equated as the intensity of the grooming response, did not result in differences in numbers of EF dropped per moose in this study. 'Sensitive' moose groomed earlier and removed more hair during the primary infestation than less sensitive moose, but total numbers of EF recovered were similar between all moose. The large number of EF recovered from MO 55 in 1982 may have been due to an acetabular abnormality which inhibited some grooming behaviors. She was also receiving daily treatments of pain killers (Phenylbutazone, Phenylbutazone, Agri-Vet Pharmaceuticals, Ltd, Western, Ontario) for most of the winter, which may have affected her sensitivity to the ticks.

All experimental moose were housed outdoors and the pens, hence, the EF, could have been accessible to small rodents and birds, both of which prey upon EF as they drop (Wilkinson, 1970; Short and Norval, 1982). However, mice were uncommon in the barn during this study (pers. observ.) and none were encountered when examining the straw bedding for EF and birds large enough to prey on EF were only rarely seen in or around the pens. It also seems improbable the mice could have consumed enough EF to account for the very low variability in the numbers of EF recovered between infestation techniques or between years of this study. Although predation of EF could have occurred, it was felt that the almost all EF in the pens were recovered and that predation by mice and birds was insignificant in this study.

Other explanations for low recovery rates of EF ticks have been proposed. Hunter and Hooker (1907) and Gladney et al. (1973) concluded that the numbers of EF *B. microplus* recovered from cattle was dependent on the nutritional quality of the ration with more ticks recovered from cattle on poor quality rations. Numbers of EF *B. microplus* on cattle restrained from grooming were higher than on unrestrained cattle (Snowball, 1956; Reik, 1962). Bennett (1969) found that the numbers of EF *B. microplus* recovered was dependent on the resistance status of the host. Susceptible animals

yielded more than 10% of the applied larvae as EF, while moderately and highly resistant animals yielded 2-5% and less than 1%, respectively. Because moose in this study were on a high nutritional plane and there was low variability in numbers of EF recovered per moose, it is speculated that a behavioral response (i.e., grooming) limited the number of EF that dropped from moose and that moose accidentally ingested many ticks during grooming bouts.

The seasonality of the drop-off period of EF has not been studied extensively, although drop-off rythms of EF ticks in response to photoperiod (George, 1971) and other factors have been examined (Hadini and Rechav, 1969; Wharton and Utech, 1970). Patrick and Hair (1977) proposed that the engorgement behavior of *A. americanum* was a photoperiodic response. In the present study, EF *D. albipictus* dropped from captive moose from late Feburary to mid-May with the peak of drop-off in late March. The synchrony of peak drop-off between animals and years indicates that the seasonal pattern of EF drop-off, especially the peak, may be influenced by photoperiod, supporting the ideas of Patrick and Hair (1977).

Ecological and biological rhythms occur in the activities of instars of many species of ticks including some aspects of host finding, feeding, morphogenesis, detachment, and egg laying (Belozerov, 1982). Seasonal rhythms are critical to synchronize tick activity with favorable environmental conditions and may be caused by photoperiod. Diapause, in its many forms, may be utilized to ensure that development occurs during the appropriate season of the year.

In addition to possibly cueing EF drop-off, photoperiod is possibly strongly influential in the onset of many activities in the life cycle of winter ticks including oviposition, larval activity, and nymphal feeding. One adaptive advantage of a photoperiodic cue for these activities is the constancy of the cue which could synchronize development with the most favorable environmental conditions on a long term basis.

Recent studies on the seasonal activity of ticks have concluded that many factors may be involved in regulating tick activity (Gregson, 1951; Sonenshine et al. 1966; Eads and Smith, 1983). These authors generally agree that the activity period of ticks is tightly controlled to occur only at specific times of the year despite large variations in annual weather conditions. I speculate that this 'rigid programming' is related to photoperiod.

F. Epizootiology of winter ticks and management implications for moose

Most of the problem areas with *Dermacentor albipictus* in Alberta lie in the aspen parkland ecotone between the prairie and boreal forest biomes (Samuel, unpub). This ecotone is characterized by large expanses of bogs intermingled with areas of aspen forest and grassland and provides excellent habitat for moose, and apparently, for winter ticks. This ecotone extends northwest into British Columbia and east into Saskatchewan, and tick problems on moose have been reported from both northeastern British Columbia (Harper and others, per comm), and western Saskatchewan (Brewster, per comm) in recent years.

There appears to be some factor or combination of factors within the ecotone in Alberta that either initiates tick outbreaks or predisposes moose in the area to large numbers of ticks. Interactions between high moose populations and favorable spring and summer weather for tick reproduction are probably the underlying cause of the problems seen in Alberta in recent years (see Samuel and Barker; 1979; Glines, 1983). A discussion of the interactions of these factors, coupled with transmission models is provided in an attempt to explain how the current tick outbreak occurred as well as some of the management implications for both moose and ticks.

The current tick-related die-off of moose in EINP began in the winter of 1976-77. Tick populations per moose varied annually, but increased from 24,000 in 1977-78 (Samuel and Barker, 1979) to over 80,000 in 1981-82 (Samuel, unpub), and declined to about 25,000 in 1982-83, suggesting the outbreak completed a full cycle during that time. The decline in tick numbers in 1982-83 suggests that the outbreak of ticks may be near its end.

Data on ungulate populations at EINP are often unreliable due to collection techniques, variable weather conditions during aerial surveys, and incomplete coverage of the total park area. This problem is currently being assessed (Blyth, per comm), and only general estimates and population trends will be used in this discussion.

Moose populations in EINP have always been high, although they have been subject to periodic fluctuations (Willman, per comm). Carrying capacities for moose and wapiti are estimated at 300-400 and 500-600, respectively (Blyth, per. comm.). Because there are no large carnivores in the park, periodic slaughters and removal of moose and wapiti

are carried out by the warden staff to maintain animal numbers within the limits imposed by the carrying capacity of the available habitat.

After the three slaughters from 1968-70, moose populations were estimated at 400-500 in the early 1970's and reached a peak of about 700 in 1977. Three slaughters were conducted from 1977-80 to control the high moose population. Populations dropped to approximately 100 animals following the severe winter of 1981-82 and numbers are currently (1983) estimated at 150-200.

The severe winter conditions of 1981-82 and malnutrition appear to be the major causes of the decline in the moose population seen in 1982-83. The influence of ticks in this die-off cannot be excluded because snow depths (approximately 50 cm) were not near critical depths for moose (approximately 100 cm, see review of Telfer, 1970), and tick numbers on moose found dead averaged 90,000 while numbers on moose shot as part of monthly research collections averaged 43,000 (Samuel, unpub).

Wapiti experienced a similar population increase in the early 1970's, but apparently suffered a major die-off in 1974 with numbers falling from 600 to 200-300 animals. Since 1976, wapiti numbers have increased markedly, but population levels have remained around 500 due to an intensive trap and removal program each winter.

The major limiting factors on the population of winter ticks are probably date of snow melt in spring, summer temperatures, date of first snowfall and associated cold temperatures in autumn, and the numbers of available hosts. The date of snow melt determines the numbers of EF that survive to lay eggs, while summer temperatures determine the number of eggs that hatch, the timing of the hatch, and larval activity. The average dates of snow melt and first snowfall are approximately 20 April and 20 October, respectively (Table 11). Variations in these dates are probably the most influential factors in determining the infestation level of moose each winter.

Dates of snow melt and snowfall, combined with a high moose population, may have been important in initiating the present tick outbreak. Dates of snow melt and first snowfall were early and late, respectively, in both 1976 and 1977 (Table 11). Snow melt in 1976 and 1977 was about 10-15 days early which would have enabled a larger number of EF to survive and lay eggs. First snowfall was about 30 days late in both years, which would have allowed a longer exposure period in autumn and enabled more moose to

acquire more ticks.

In at least two of the five years from 1978-1983, weather conditions in spring and summer appeared to influence numbers of ticks per moose. Dates of snow melt and first snowfall were fairly 'normal' in 1978 and 1979 (Table 11), but weather conditions in 1980 and 1981 allowed large increases in the tick population. In 1980, snow melt occurred about one week early, while snow melt in 1981 occurred on 24 March, one month before the 30 year average of 20 April (Table 11). Because the snow cover was gone before the peak of the EF drop-off in 1981, the numbers of EF that survived and laid eggs in spring and the numbers of larvae available to moose in autumn must have been very large to account for averages of over 80,000 ticks per moose in 1981-82 (Samuel, unpub).

In order to understand the influence of various factors in the epizootiology of *D. albipictus* in EINP, transmission models were constructed using the basic concepts of Leong (1975), Holmes et al. (1977), and Kralka (1983). Answers to the following questions were sought: 1) Which host species contributes the greatest number of EF in spring? 2) Which habitat type receives the greatest number of EF in spring? 3) Which host species receives the largest proportion of the larvae in autumn? 4) Which habitat type contributes the greatest number of larvae for transmission in autumn?

Parasite flow rates were not measured, but were derived from a static distribution of host populations and reproductive performance of *D. albipictus* under field conditions in EINP. Calculation of relative flow rates of ticks must consider a number of factors, therefore, calculations were organized in a 4x3 matrix of the four ungulate host species and the three habitat types (see Appendix 9 for calculations). Cells for calculation of flow rates of EF between hosts and habitats included host density, habitat usage by each host species, the proportion of each habitat type in EINP, the abundance of ticks on each host species, and a constant factor for the proportion of EF that drop from each host species. Cells for calculations of flow rates of larvae between habitats and hosts included all the above as well as EF survival rates, number of eggs produced per EF, and percent egg hatch.

The assumptions used in the calculations and the model are as follows:
1) Host populations are stable and at or near the carrying capacity for EINP and are

estimated at 500 wapiti, 400 moose, 300 deer, and 600 bison.

2) Habitat usage by each host species is similar to Cairns (1976).

3) Succession is static and the relative proportions of each habitat type in EINP is unchanged from Cairns (1976).

4) All hosts yield 1.5% of their tick population as EF.

5) Reproductive parameters of EF from all host species are similar to moose-source EF used in the present study.

6) All larvae that hatch become available for transmission in autumn.

Using these calculations and assumptions, moose contribute 71% of the EF population in spring, while wapiti contribute 25% (Fig. 23). The contribution of EF from deer and bison is negligible. Approximately 97% of all EF are dropped in the aspen habitat. The habitat preferences of moose and wapiti (Cairns, 1976), as well as the dominance of the aspen cover type in EINP (Cairns, 1976; per. obser.) are probably responsible for the large proportion of EF in this habitat type.

Based on reproductive data from EF in the present study, all hosts receive approximately the same relative proportion of the available larvae in autumn as the proportion of EF each contributes in spring (Fig. 23). Moose receive the largest proportion (68%) of the larvae available in autumn. It is uncertain if this is due to an attraction of larvae for moose or to the synchrony of host and larval activity periods as discussed previously. Eighty four percent of the available larvae are in the aspen habitat (Fig. 23). If the assumption of no differential reproduction of EF due to host species is correct, moose are the dominant host in regulating the total population of winter ticks in EINP. The aspen habitat is the major site of transmission with more than 75% of the available larvae present in this habitat type.

If moose populations are low (100 animals), wapiti become the dominant host for tick flow to and from the total tick population in EINP (Fig. 24). The aspen habitat would continue to receive the majority of EF in spring and contribute the majority of larvae available in autumn (Fig. 24), but the grassland would contribute a larger proportion of the larvae than in a moose driven cycle.

Further work is needed to determine the reproductive performance of EF from other host species under field conditions to verify these relative flow rates. Habitat usage

Figure 23. Relative flow rates between ungulate hosts and habitat types
in Elk Island National Park, Alberta, assuming ungulate
populations at carrying capacity. Solid arrows indicate
flow of engorged females in spring and open arrows indicate
flow of larvae in autumn.

DEER
0.038   0.038   0.682   0.711
MOOSE

DERMACENTOR ALBIPICTUS

0.001   0.001   0.250   0.279

BISON   WAPITI

ASPEN   BOG
0.970   0.840   0.006   0.030

DERMACENTOR ALBIPICTUS

0.024   0.131

GRASSLAND
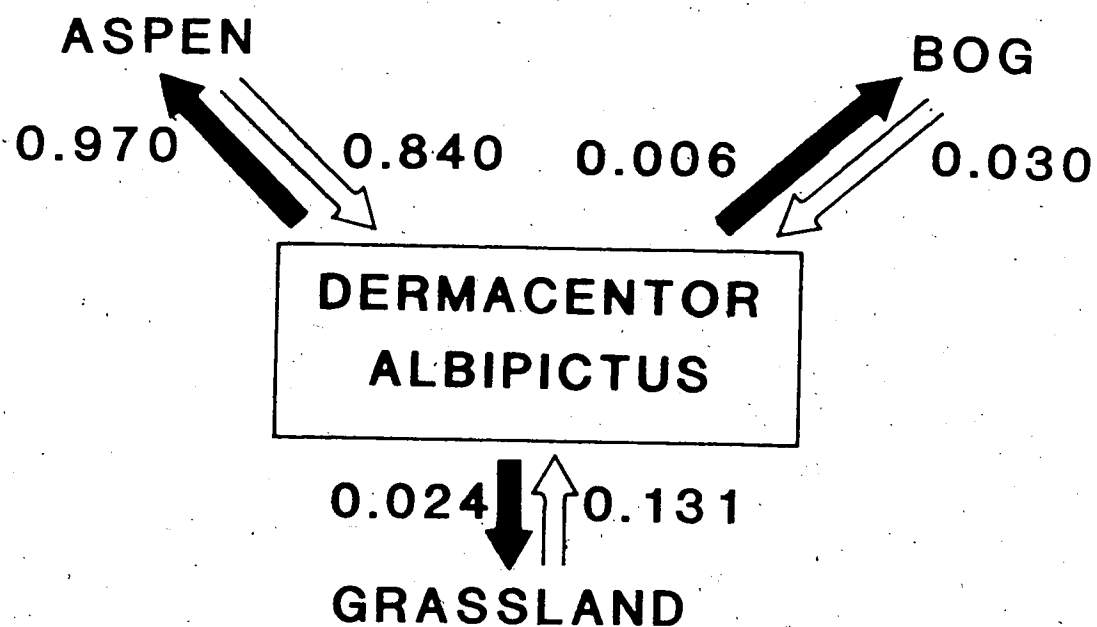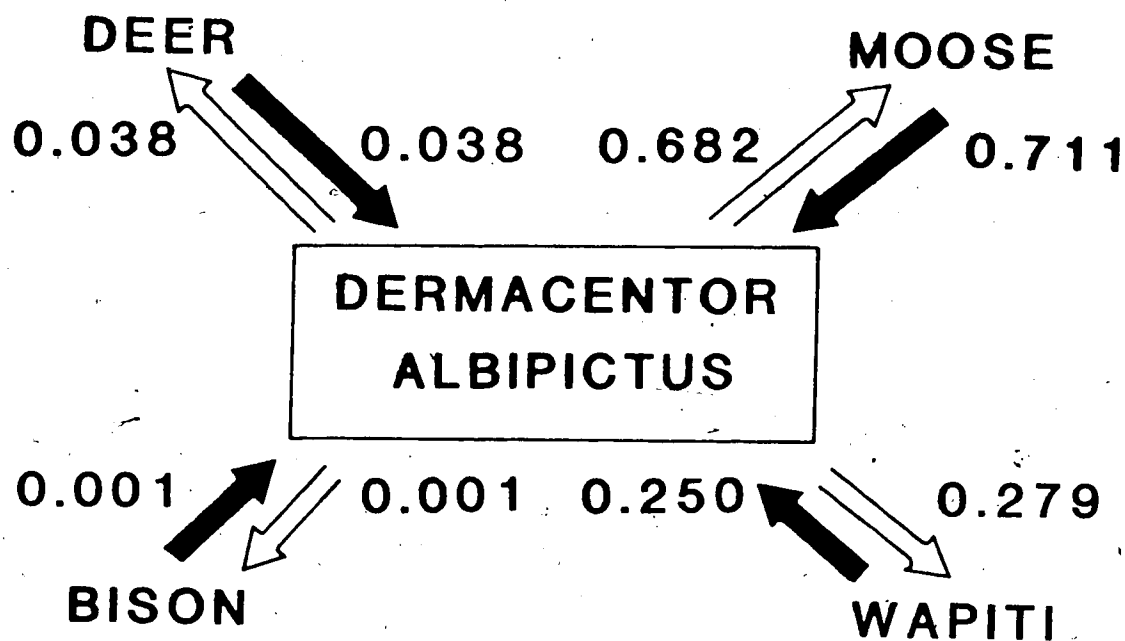
Figure 24. Relative flow rates between ungulate hosts and habitat types

in Elk Island National Park, Alberta, assuming low moose

populations and all other ungulate populations at carrying

capacity. Solid arrows indicate flow of engorged females

in spring and open arrows indicate flow of larvae in

autumn.

DEER 0.176 0.081 0.358 0.381 MOOSE

DERMACENTOR ALBIPICTUS

0.002 0.002 0.536 0.563

BISON WAPITI

ASPEN 0.964 0.786 0.005 0.030 BOG

DERMACENTOR ALBIPICTUS

0.031 0.192

GRASSLAND
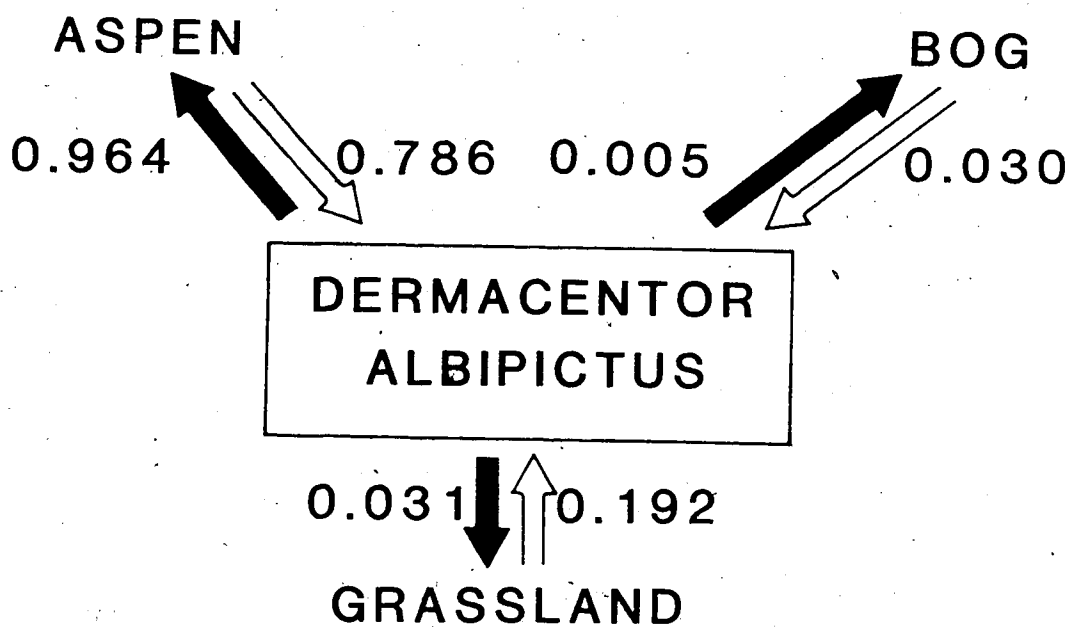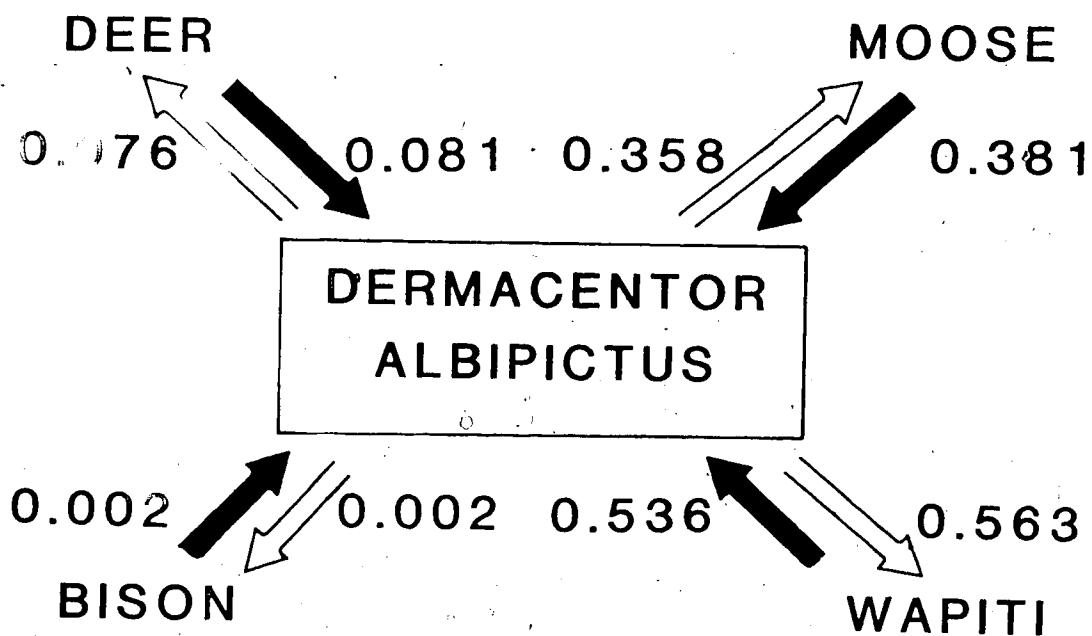
by each host species in March-April and October-November is also needed to fine tune and increase the accuracy of the flow rates between each host and habitat.

A predictive equation was derived for estimating the numbers of larvae available to moose in EINP each year from 1978 to 1983. Three assumptions, in addition to those made for the transmission models, were made for this equation:

1) Reproductive performance of EF in all habitat types was similar in all years to those found in the present study (1982).

2) All animals infested in autumn survived and dropped EF the following spring.

3) All larvae that hatch are acquired by a host.

$$L=[(N)(\%EF)(S^1)(D^1)+(N)(\%EF)(S^2)(D^2)](\#eggs/EF)(\%hatch)(P)(U)$$

where: L = the total number of available larvae in autumn; N = the mean number of ticks per host individual the previous winter; %EF = 0.015 (the mean percent yield of EF from captive moose); D^1, D^2 = the proportion of EF that drop-off before and after snowmelt, respectively (Appendix 10); S^1, S^2 = the mean survival of EF before and after snowmelt, respectively (0.12 and 0.60, 0.037 and 0.256, and 0.093 and 0.733 for the bog, aspen, and grassland, respectively); P = the proportion of each habitat type in EINP (after Cairns, 1976)(aspen forest + shrubland = 0.79, bog = 0.07, grassland + shrub meadow = 0.14); U = the relative usage of each habitat in EINP by each ungulate species (after Cairns, 1976)(aspen forest + shrubland, bog, and grassland + shrub meadow).

Equations for numbers of larvae in each habitat (L^1=bog, L^2=aspen, L^3=grassland, L(t)=total) become:

$$L^1=[(N)(.015)(.12)(D^1)+(N)(.015)(.60)(D^2)](3227)(.51)(.07)(.06)$$
$$L^2=[(N)(.015)(.037)(D^1)+(N)(.015)(.256)(D^2)](3013)(.23)(.79)(.85)$$
$$L^3=[(N)(.015)(.093)(D^1)+(N)(.015)(.773)(D^2)](3153)(.59)(.09)(.14)$$
$$L(t)=L^1+L^2+L^3$$

By multiplying L(t) by the number of moose in March-April (X) and dividing by the number of moose in October-November (Y), a predicted infestation level per moose (Z) can be calculated:

$$Z = [L(t)(X)] / (Y)$$

Using these equations, data on moose populations in EINP (Blyth, unpub), and average tick loads per moose from 1977 to 1983 (Samuel, unpub), infestation levels reasonably close to that found by digestions of hides from moose were obtained for three of the five years (Table 15). In the first exception, numbers of ticks per moose increased from 9679 in 1979-80 to 45,720 in 1980-81 (Samuel, unpub). Using the 1979-80 infestation level, estimated tick loads per moose in 1980-81 were about 16% that found by hide digestion (Table 15). The reasons for this discrepancy are unknown, but one possible explanation is that only six hides were digested in 1979-80 (Glines, 1983) and the actual infestation level may have been underestimated. Weather conditions in spring, 1980 should have resulted in a decrease in tick numbers per moose the following autumn. Snowmelt date in 1980 was normal, but early summer temperatures were lower than average (Table 11). The low temperatures should have decreased the number of degree hours over 15°C and, thus, decreased the percent egg hatch and, subsequently, the numbers of larvae available in autumn, 1980.

Predictions for 1983 greatly exceeded the average tick load from hide digestions (Table 15). This prediction is probably high for a number of reasons: time specific mortality rates for moose in late winter 1981-82 are not known; many moose died before dropping large numbers of EF (per. observ.); and possible underestimation of tick numbers because only seven hides were digested. Further investigation on the effects of annual differences in summer temperatures and time specific moose population data are needed to verify the predictive value of these equations.

In an attempt to assimilate data from the present study into a workable model, a flow diagram emphasizing potential interactions between moose and ticks was devised. The flow diagram (Fig. 25) is assumed to operate on a host density dependent basis. If moose are the primary host in natural cycles of winter ticks, the cycle is proposed to operate in figure-8 manner, oscillating between high moose populations with high tick loads per moose and low moose populations with low tick loads per moose. The period

Table 15. Comparison between infestation levels of <u>Dermacentor</u> <u>albipictus</u> on moose as determined by hide digestion and predicted numbers of ticks in Elk Island National Park, Alberta.

Year	No. of Hides	$\bar{X}$ No. Ticks per Moose[a]	Predicted No. Ticks per Moose[b]
1977-78	28	23,240	----
1978-79	--	------	23,268
1979-80	6	9,679	14,959
1980-81	21	45,720	7,089
1981-82	10	80,664	82,476
1982-83	7	24,038	74,990

[a] Data of Samuel (unpub).

[b] See text for details of calculations.

Figure 25. A flow diagram of the interactions between moose, habitat,

and weather at Elk Island National Park, Alberta.
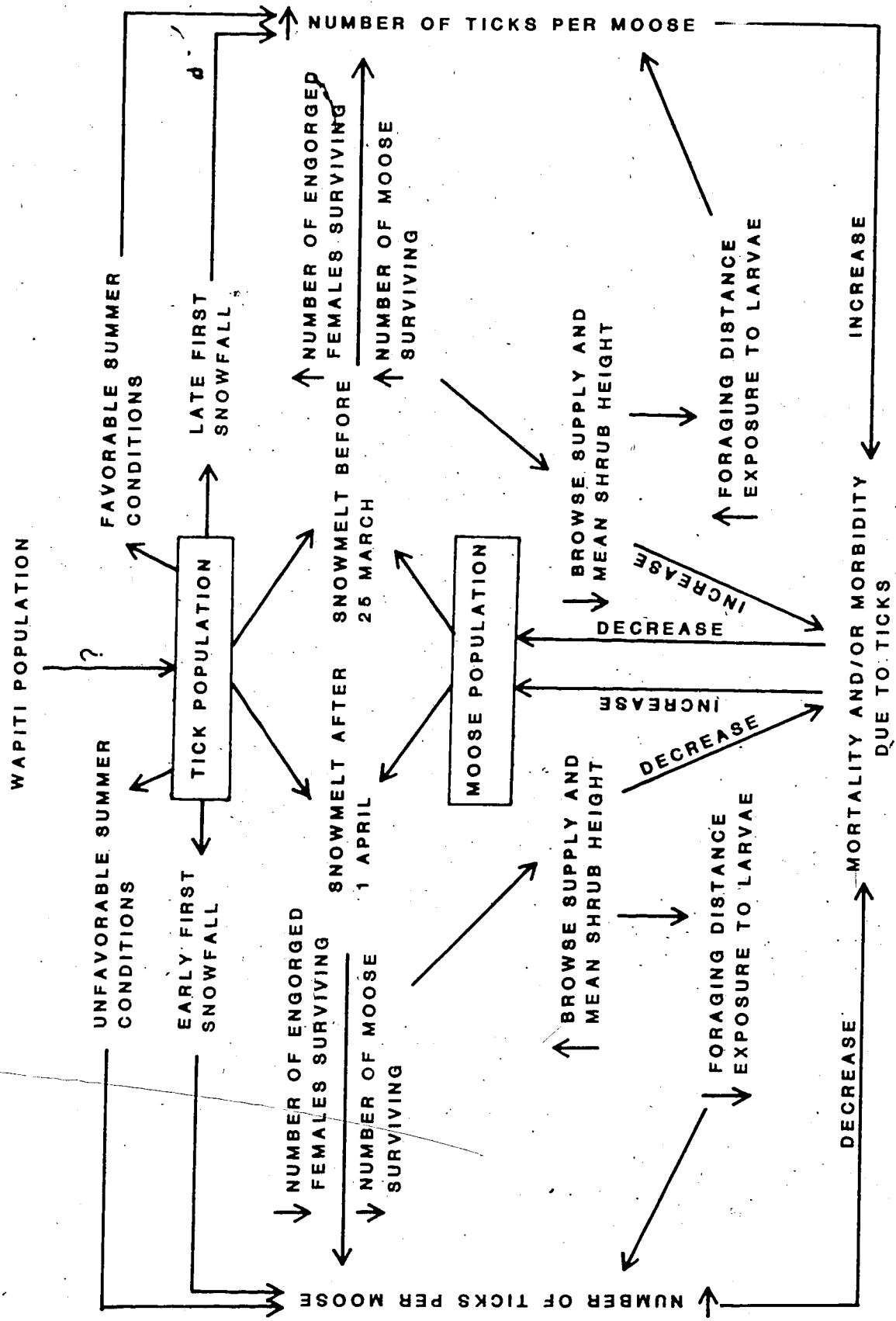
of time spent at the upper end is dependent on the length of time before a malnutrition/tick-induced mortality factor causes a major decline in the moose population. A series of years with late springs and early autumns may cause a temporary decline in the tick population, but unless host density declines, no major reduction in tick numbers per moose is foreseen.

The effect of a high wapiti population on the suprapopulation of winter ticks is unknown. Wapiti are more versatile feeders than moose and can browse or graze depending on food availability. These feeding patterns could affect movements and behavior of wapiti at critical times of the year for ticks. Therefore, interactions between winter ticks and wapiti populations may not undergo a similar flow pattern as in Fig. 25. Due to the high population at EINP, wapiti are approaching total substitution for moose as the primary host in the population dynamics of the tick population. They will probably continue to do so until moose populations build and acquire the majority of the tick population again. The effect of a tick cycle dominated by wapiti on tick numbers, grooming, and subsequent hair-loss of moose is not known.

Because the life cycle of *D. albipictus* appears strongly influenced by photoperiod and environmental conditions, there are several 'windows' during which control efforts could be made. Burning between snow melt and spring green-up to kill EF prior to oviposition or in autumn between mid-September and early October to kill larvae may be very effective in controlling numbers of ticks available to moose (see Appendix 11).

The other area of potential control and management for ticks is in the regulation of potential host populations. *D. albipictus* seems to prefer moose over wapiti and deer as evidenced by large differences in tick loads on these hosts (Samuel, unpub). Moose may be the most important host for tick population dynamics in naturally occurring systems, but on a population level, the contribution of each potential host species to the total number of ticks (Fig. 23 and 24) must be recognized. Therefore, the total population of each host species probably plays an important role in the dynamics of the tick population. This is especially important when considering the habitat preference of each host and the overlapping usage of habitat types. Interspecific interactions, especially when populations of all three major host species are high, may markedly affect the exposure level of all ungulates in the park by exclusion or inclusion of particular species to certain

areas or habitat types in the park.

Host-stocking densities also play an important role in the acquisition rate of ticks by hosts (Sutherst et al. 1977). With higher densities of potential hosts, the probability of a host encountering a clump of larvae is increased. The net effect is that a larger proportion of the available larvae would be acquired by a host, increasing the overall infestation levels.

Environmental conditions in summer, especially temperature, probably determine the numbers of larvae available for transmission. However, the number of larvae available for transmission also depends on the numbers of EF that survive in spring and that in turn, depends on the host stocking density the previous autumn and the date of snowmelt. In this way, an ever increasing spiral of host numbers and tick numbers could be achieved. Because most EF are dropped in the aspen habitat (Fig. 23) and the aspen habitat provides the largest proportion of available habitat in EINP (Cairns, 1976), any change in the characteristics in this habitat type (i.e., burning, logging, etc.) would have a great influence on the tick population.

Wildlife managers can exert very little control over weather conditions, but the complex relationship between weather conditions and tick populations should be included in all management programs for moose in central Alberta. A monitoring program for dates of snow-melt, degree hour summations over 15°C from 1 June to 1 September, and first snowfall should be instituted. If these measurements indicate a high reproductive potential for ticks, tick reduction programs or moose reduction (hunting) programs should be instituted, if desired.

All animal populations fluctuate both annually and over time. Annual increases in populations occur during the reproductive season, but the limits to population growth in northern and temperate areas are usually imposed by food availability during winter (Keith and Windberg, 1978; Gasaway et al. 1983). Over the long term, populations of ungulates are assumed to be relatively stable, at least if they are in natural situations. The absence of predators probably contributes more to the over-population of ungulates than any other factor. In order for populations of *Dermacentor albipictus* to be maintained at 'natural' levels, populations of its primary host(s) must be controlled. Management of moose populations by hunting would appear the most feasible approach to altering and controlling

tick levels in central Alberta.

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APPENDIX 1. Techniques for raising moose calves (<u>Alces</u> <u>alces</u>) in captivity.

(To be submitted to the Journal of Wildlife Management, 1984).

Raising neonatal ungulates by hand is one of the only ways to ensure healthy, tractable animals for use in experimental studies in many aspects of wildlife management. However, the process in difficult, time consuming, and often unrewarding due to high mortality rates. In North America, many reports on methods for raising neonatal deer (*Odocoileus virginianus* and *O. hemionus*) have been published (Long et al. 1961; Silver, 1961; Trainer, 1962; Reichert, 1972; Buckland et al. 1975; Halford and Alldredge, 1978; Pybus, 1983), but no preferred or universal methods have been adopted.

Techniques for raising other species of ungulates such as caribou (Jones, 1966), red deer (Youngson, 1970), pronghorn (Schwartz et al. 1976), and wapiti (Hobbs and Baker, 1979; Gates, 1980) have also been reported. The small number of reports for raising these species may be due to a lower demand for experimental research with these species or to the difficulty in raising them successfully by hand.

Although a number of reports of techniques for raising moose calves exist (Dodds, 1959; Markgren, 1966; Landowski, 1969; Regelin et al. 1982; Lautenschlager and Crawford, 1983; Addison et al. 1983), only Addison et al. (1983) reported successfully raising more than six calves. This paper reports techniques developed over five years to successfully raise and train moose for experimental studies on the life cycle of winter·ticks (*Dermacentor albipictus*) in Alberta.

MATERIALS AND METHODS

Raising techniques

From late May to mid-August, 1981 and late May to mid-June, 1982, 30 moose calves were obtained from various parts of Alberta through the cooperation of Alberta Fish and Wildlife Division officers. Thirteen calves were captured using a helicopter between 29 May and 5 June and 17 were submitted as "orphans".

Upon entry to the facilities at the University of Alberta Biomedical Animal Center at Ellerslie, all animals were given a thorough physical examination and checked for wounds and other signs of trauma. A detailed history, including date and location when found, feeding schedules, and notes on behavior and activites was compiled for each animal. Calves received after 10 June were isolated for three to five days for observation of

infectious diseases and to check for internal helminths by fecal examinations.

Calves were housed in concrete-floored pens side a heated barn. Each pen had an adjoining outdoor, concrete runway and calves were allowed outside during favorable weather after the first week. Calves were allowed access to a grassy paddock after halter training had begun, usually four to five weeks after receipt.

Dirt and water were available at all times during the pre-weaning period. Alfalfa/timothy hay and fresh aspen (*Populus tremuloides*) browse were offered after three to four weeks.

All calves were bottle-fed a milk formula of one part whole, unpasturized bovine milk to one part evaporated milk. When available, 160 ml (4 oz) of bovine colostrum was added to the formula at each feeding. All calves were fed on a predetermined schedule (Table 1). Daily volumes changed from 1981 to 1982, but frequency of feeding was the same. Advances in the feeding schedule were based on animal health and weight gains. A powdered vitamin supplement (Pervinal, 8 in 1 Pet Products, St. Aubrey, NY) was occassionally mixed into the formula. Milk was warmed to body temperature before each feeding.

Detailed records of amount of formula consumed, defecation, urination, activities, and general condition were recorded for each animal after each feeding. All calves were weighed twice weekly until weaning and once per week after.

In 1981, the transition from milk to solid food was encouraged by mixing an increasing proportion of rolled oats into the dirt. The rolled oats were gradually replaced with an increasing proportion of a pelleted aspen ration (Table 2) to which all calves were eventually weaned. In 1982, a commercially available, 18% crude protein, dairy creep ration was used instead of the rolled oats and the aspen pellets were replaced by a custom prepared alfalfa-based pelleted ration (Table 2) as the post-weaning ration. This ration was replaced in December, 1982 by the alfalfa-based pelleted ration (Table 2) that was fed to experimental deer housed in the same facility.

Cleanliness was considered very important. All bottles and nipples were rinsed immediately after each feeding. Bottles were sterilized in the steam cycle of a dishwasher and nipples were immersed and stored in a disinfectant bath until the next feeding. All personnel involved in raising the calves were required to wear coveralls and rubber boots

Table 1. Feeding schedule for moose calves raised at the University of Alberta Biomedical Research Center, 1981-1982.

Year	Volume per feeding		Frequency (times/day)	Duration	Total Volume Per Day	
	ml	oz			ml	oz
1981	397	14	6	1 week	2381	84
	454	16	6	1 week	2722	96
	624	22	5	5 days	3119	110
	680	24	5	5 days	3402	120
	737	26	5	2-3 days	3686	130
	964	34	4	1 week	3856	136
	1020	36	3	10 days	3062	108
	907	32	3	1 week	2722	96
	851	30	3	1 week	2552	90
	1077	38	2	11 days	2155	76
	1077	38	1	1 week	1077	38
1982	340	12	6	2 weeks	2041	72
	397	14	6	1 week	2381	84
	510	18	5	1 week	2552	90
	567	20	5	1 week	2835	100
	737	26	4	1 week	2948	104
	851	30	4	1 week	3402	120
	794	28	3	1 week	2381	84
	680	24	3	1 week	2041	72
	851	30	2	1 week	1701	60
	680	24	2	1 week	1360	48
	851	30	1	1 week	851	30

Formula was a 1:1 mixture of whole bovine milk:evaporated milk.

Table 2. Composition and nutrient analysis of pelleted rations fed to captive moose at the University of Alberta Biomedical Research Center, 1981-1983.

Year Used	1981-82	1982	Dec. 1982 - ? (Deer Pellets)
Pellet Base	Aspen	Alfalfa	Alfalfa
Ingredients (kg/1000 kg feed)			
Dehydrated Alfalfa	---	400	255
Barley	400	300	310
Aspen Sawdust	200	---	---
Oats	175	210	---
Shorts	---	---	140
Beet Pulp	75	26	160
Soybean Meal	75	40	85
Molasses	35	---	40
Dical Phosphorus	13	5	---
Trace Mineral Salt	7	3	4
Vitamin A, D, E	3	1	2
Moldcurb	1	---	---
Permopellet	12	1.	1
Composition (as fed basis)			
Moisture (%)	9.3	8.2	11.2
Protein (%)	13.1	12.8	17.9
Fiber (%)	17.8	19.3	14.9
Calcium (%)	0.46	0.90	0.84
Phosphorus (%)	0.56	0.36	0.44
NO_3^- (%)	---	0.08	---
Magnesium (%)	15	0.20	0.26
Potassium (%)	0.77	1.02	1.22
Copper (ppm)	7.7	10.9	10.9
Manganese (ppm)	55.0	42.8	57.0
Zinc (ppm)	61.3	54.4	59.0
Selenium (ppb)	159	142	295

while on the premises. Foot baths containing a cresote disinfectant were used immediately after entry into the barn from the outside and after entry from any outside paddock. A separate set of coveralls and rubber boots was used exclusively for handling animals in 'sick bay'. Clothing was changed prior to and after handling sick animals.

Treatment of illnesses

Sick calves were isolated from all other animals in the barn until they recovered or died. Illness was usually first noted as listlessness or refusal to feed. Rectal temperatures of animals that did not feed normally or were listless were taken immediately after the feeding and the animal was moved to sick bay if the temperature was higher than 39.2°C.

Temperatures over 39.4°C were regarded initially as fever due to a bacterial infection and treated intermuscularly with a progression of antibiotics from penicillin G (Ethacillin, Rogar/STB, London, Ontario), chloramphenicol (Austicol 200, Austin Laboratories, Joliette, Quebec), and oxytetracycline hydrochloride (Liquamycin, Rogar/STB, London, Ontario). Penicillin was usually effective and temperatures usually returned to normal in two to three days.

Bloat was occasionally encountered after feeding in 1981, possibly due to very rapid ingestion of milk through nipples with large openings, or to slightly sour milk or sour colostrum used in the formula. Calves with bloat were treated with dioctyl sodium sulfosuccinate (Bloat-go, Animal Health Supplies, LTD, Regina, Saskatchewan) administered each feeding and/or a bismuth subsalicylate suspension (Pepto-bismol, Norwich-Eaton, Paris, Ontario) given in 10-20 ml doses at two hour intervals. Milk volumes were reduced by 1/2 for the first two to three feedings after the animal bloated and replaced with electrolytes (Calf Electrolytes, Salsbury Laboratories, LTD, Kitchner, Ontario) in severe cases. Occasionally, calves with severe bloat were stomach tubed and the sour milk and other rumen contents removed. All animals were walked as often as possible. Lacto-bacillus tablets (Bacid, USV, Mississauga, Ontario) were adminstered occasionally and found to be partially effective against bloat.

Mineral oil was used to successfully treat the one case of constipation.

Diarrhea was the most frequent, persistent, and difficult problem to treat. In 1981, treatment consisted of immediately decreasing the milk volume by half for two to

three feedings and giving neomycin sulfate and methscopolamine bromide (Biosol-M, Tuco Products Co. Orangeville, Ontario) orally after each feeding. Persistent or severe cases were given partial or complete substitution of milk with electrolytes and glucose with oral treatments of 5-10 ml of an opium, kaolin and pectin suspension (Donnegel-PG, A.H. Robbins Co., Montreal, Quebec) twice per day and/or oral treatments with 20-50 ml of kaolin and pectin (Kaopectate, Tuco Products Co., Orangeville, Ontario) twice a day. Early detection and the decrease in milk volume was usually effective, although few calves had pelleted feces until after weaning.

Diarrhea was treated differently in 1982 because an unusually severe and widespread gastro-intestinal infection was encountered. One calf had diarrhea on 1 July and by 6 July all 16 calves in the barn were scouring severely. All milk was replaced with 900 ml (32 oz) of an oral nutrient powder mixed in water (Life-guard, Norden Co., Calgary, Alberta) each feeding for five to seven days and various oral treatments were given including suspensions of: 1) bismuth subsalicylate, kaolin and pectin; 2) streptomycin, sulfamethazine, kaolin and pectin, and aluminum oxide suspension (Sul-Dyo-Strep, Pfizer Co. LTD, Montreal, Quebec); 3) dihydrostreptomycin, sulfamethazine, kaolin, pectin, salts, and aluminum hydroxide (Hibitane, Ayerst Laboratories, Montreal, Quebec), and; 4) opium, kaolin and pectin. Boluses of chlorhexidine, hydrochloride, dihydrostrepomycin, kaolin. and sulphamethazin salts (Polyansyne, Ayerst Laboratories, Montreal, Quebec) were also given. None of the treatments was particularily effective, therefore milk was gradually reinstituted into the formula after five to 10 days of treatment and the diarrhea in all calves cleared up within two to three weeks after the onset. Only minor problems with diarrhea were encountered afterwards.

Superficial cuts, wounds, and srcapes were treated by cleaning with hydrogen peroxide and applying a topical disinfectant containing chlorohexidine acetate (Hibitane, Ayerst Laboratories, Montreal, Quebec).

Extensive intravenous feedings and treatments were utilized to combat a prolonged period of endotoxemic shock in two calves in 1982. Both calves dropped in body temperature to 37-37.5°C and, occassionally, lost consciousness. Continous drip feedings of 10% glucose and saline and treatments with large doses of prednisolone sodium succinate (Solu-Delta-Cortef 100, Tuco Products Co., Orangeville, Ontario) and

chloramphenicol were used for two to three days twice on one calf and four times on the other. Both calves recovered.

Training

Halter training was begun at two to three weeks of age. Rope halters of 0.6 cm (1 / 4 in) hemp were constructed. These halter were used until weaning by adjusting the length of the noseband to accommodate growth. Larger halters of 1.3 cm (1 / 2 in) hemp were constructed for use after weaning. Leather and nylon horse halters were used after weaning in 1982 and for all yearling moose. Lead ropes with a section of small link chain (stallion leads) for wrapping around the nose were used for the yearling bulls during and after the rut.

Halter training was accomplished in many slow steps. Calves were initially habituated to the rope halters by putting the halter on for a few hours each day at about two weeks of age. After becoming used to the halters, calves were not allowed to leave the pens without being haltered.

Calves were taught to lead by being haltered and led to and from the weigh scale for the twice weekly weighings. When access to the grassy paddock was permitted, all calves were haltered and led to and from the paddock. This portion of the training was facilitated by the use of rewards: access to the paddock to 'play', fresh browse upon return to the barn, and a liberal supply of bananas.

Calves were taught to stand tied to a post or fence by tying the lead rope of the halters to the sides of the pens during feedings. They were tied five to 10 minutes before feeding and released 5 to 10 minutes after feeding. This was necessary for later experimental work and also to prevent injury to workers by over-eager, hungry calves during feeding.

After weaning in 1981, training sessions became less frequent and eventually led to behavioral problems during later experimental work. To combat this problem, half hour training sessions were conducted with each moose two to three times per week from December, 1981 to May, 1982. Training sessions in 1982 were conducted from September, 1982 to May, 1983. Sessions for the three yearling bulls and one yearling cow were conducted three times per week during the summer of 1982 and two to three times per week throughout the experimental work in 1982-83.

Firm discipline was essential to the training process. Discipline was usually adminstered in the following order: voice, hand, and rope. Discipline intensified to the point of being forceful during severe misbehavior and during the rut of the yearling males.

Various psychological and physical methods were used to establish dominance over particularily aggresssive or large calves and the yearling males. Most involved letting the moose 'fight' against an immovable object (a wall or fence) until it either tired or gave up. Once calves had submitted and were calmed, normal training procedures were followed.

The yearling males offered a special problem during the rutting season. As soon as the velvet on the antlers was removed, and before the males had sufficient time to test the length and effectiveness of their antlers, the antlers were removed. During the rut, severe discipline was administered in response to any threat display or act of aggressiveness. Dominance was established by inviting an encounter with me while I was standing at an open gate into the pen of each male. As the male advanced, he normally displayed and occasionally vocalized. When he was within reach, the gate was closed to lock the knobs of his antlers into the chain link of the gate. He was allowed to push against the gate until he tired or gave up. As soon as he backed away from the gate, the gate was opened and a sharp blow was given by hand on the nose. This usually resulted in immediate retreat and a submissive posture. This process was repeated twice on two of the three males and no problems were encountered afterwards that could not be handled with normal discpline. The third and largest male refused to submit and was sold after repeated aggresssive and dangerous encounters.

REULTS AND DISCUSSION

From 1975-1980, 25 moose calves were successfully raised at the University of Alberta Biomedical Animal Center (Glines, 1983; Samuel, unpub.). The successes and failures of techniques used during this period provided the baisis for the techniques presented here. Using these techniques, six of 13 and 11 of 15 calves were successfully raised in 1981 and 1982, respectively, attributing to the effectiveness of the system used.

Success in weaning was much higher for calves received before 10 June than for those received after 10 June for both years of this study. Five of eight calves received before 10 June survived to weaning in 1981. Two of these calves died within one week after weaning due to problems unassociated with the feeding or weaning process. Only one of five calves received after 10 June survived. Success was much better in 1982 with 11 of 15 calves received prior to 10 June surviving to weaning. The single calf received after 10 June died.

Weaning was completed by 17 August, 1981 and 7 September, 1982 for most calves. One calf in each year was kept on milk until 15 October because they were extremely small for their age, but only one survived.

Cause of death of calves that died before weaning was variable and no consistent pattern was observed. Nine of 12 mortalities that occurred in 1981 and 1982 were due to conditions that were either not treatable (i.e., trauma, spinal abscess) or non-specific, wasting conditions (i.e., nephritis, hypoproteinemia, and endotoxemia).

Only calves received after two months of age were apparently stressed by conditions at our facility. These calves did not allow as close contact with the feeding personnel as calves received at a younger age and did not accept the bottle-feeding as readily as calves received prior to 10 June. In this study, the method of capture was not linked to early mortality as noted by Addison et al. (1983) or with difficulty of feeding (Glines, 1983). Only very sick animals, one calf with an abscess on the lower mandible, and two calves received when about two months old, had to be force fed using a bottle and a nipple with a large opening to literally pour milk into the back of the throat while gently massaging the throat.

Weight gains per day and per liter of formula consumed by calves that survived were similar in 1981 and 1982 (Table 3). Calves in 1982 were smaller on arrival and at weaning, but it is not known if this difference is associated with the differences in feeding schedules or to the severe scouring problems. The difference in total milk consumed (Table 3) is due to the large fluid volumes fed during the serious scours problem in 1982. All healthy calves consumed all milk formula offered.

Comparisons of feeding schedules indicate that about 150-200 l of formula might be an optimum total volume to use for raising neonatal moose. Total milk consumed

Table 3. Weight gains and milk consumption of moose calves raised at the University of Alberta Biomedical Research Center, 1981 and 1982.

Year	n	Initial Weight (kg)	Weaning Weight (kg)	Change in Weight (kg)	Gain per Day (kg/day)	Total Milk Consumed (l)	Gain per Liter Consumed (kg/l)
1981	5	26.0 ± 5.0[a]	72.0 ± 14.4	46.0 ± 12.8	0.60 ± 0.16	204.5 ± 17.8	0.23 ± 0.06
1982	13	19.1 ± 6.4	65.7 ± 12.4	46.6 ± 10.2	0.48 ± 0.11	222.2 ± 22.0	0.22 ± 0.06

[a]Mean ± 1 SD.

varies from 120 l (Addsion et al. 1983), 210 l (present study), 260 l (Regelin et al. 1982), and approximately 600 l (Landowski, 1969). Daily volumes of milk offered and consumed are not given in most of these studies, but are assumed to reflect the total volume used. Total volumes over 250 l are probably excessive based on the success in raising moose on 210 l or less of a milk formula (Addison et al. 1983; present study). Volumes greater than this may lead to digestive problems and difficulties in weaning animals onto solid food.

Other than diarrhea, health problems in both years were usually not serious. One case of *Salmonella* spp. was diagnosed and successfully treated in 1981. A different animal acquired a *Salmonella* spp. infection in summer 1982 as a yearling and was treated and appeared to recover. One calf in both years had problems with hypoproteinemia. Both were treated with intravenous amino acid suspensions in addition to the milk formula, but neither survived.

The only serious health problem in 1982 was the short period of severe scouring in all calves. The scouring was apparently caused by an extremely resistant *E. coli* (cultured many times) and was possibly accompanied by a viral agent. It appeared host specific as only two of 35 white-tailed and mule deer fawns in the barn at the same time began scouring during and after the period that the moose calves were scouring. No calves died as a result of this scouring problem.

Some of the problems encountered during this study may be related to the pelleted ration that was fed prior to and after weaning. The pelleted aspen ration used for weaning and maintainance in 1981-82 produced reasonable weight gains, but was expensive to produce. It was mixed wrong two to three times during the year and a half that it was used and at least some of the mortality that occurred near weaning in 1981 could be attributed to this factor. The calves that supplemented their daily food intake with large quantities of hay and grass were in better condition than those that did not, suggesting that the ration was deficient in some way. The ration was analyed three times during the time it was used. It was low in protein and energy, had an improper Ca:P ratio, and near toxic levels of vitamins A, D, and E all three times (Table 2).

The new ration formulated using an alfalfa base for use in 1982 worked well for weaning and a short period after weaning, with good weight gains attained by almost all

moose. The second batch made was mixed wrong and contained a very bitter tasting compound that may have caused some of the anorexia in experimental animals in 1982-83. This ration was also low in protein, but the Ca:P ratio was in proper balance (Table 2). The commercial alfalfa-based pelleted ration (Table 2) used for experimental deer housed at the Ellerslie facility was subsituted for the moose ration in December, 1982 and food consumption and weight gains increased.

Halter training moose was very successful. The use of training sessions at early ages is thought to have been the primary reason for avoiding difficulties experienced by Lautenschlager and Crawford (1983) and the discipline problems reported by Markgren (1966). Most moose would lead with minimal resistance and all would stand calmly while tied for one half to one hour. With frequent training sessions and firm discipline, moose could be trained very similarily to horses. Only a small number of handlers (one to two) should be used, and areas with large volumes of vehicle and human traffic should be avoided because moose were easily frightened by sudden, loud, or unexpected noises, and by strange people in the immediate area.

If dominance can be established over bulls at an early age (one year) and maintained through constant training sessions, they should be tractable during all but the peak of the rut. They should be kept away from all other males and females during training sessions just prior to, during, and just after the rutting season.

Success in rearing moose calves using the methods outlined is attributed to the formula used, the small number (four to five) of people directly involved in feeding the calves, early detection of illness and other problems by having personnel in the barn 24 hours per day, access to natural vegetation and dirt, and lots of tender loving care administered constantly. It is suggested that calves not be weaned until they reach 68 kg (150 lbs) and that raising attempts be restricted to calves acquired prior to 10 June (less than three weeks of age). Halter training should begin as early as possible and continue throughout the experimental life of the animal to ensure control over all animals.

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APPENDIX 2. Annual trends in maximum and minimum temperature, precip-

    tation, and cumulative snow cover for Elk Island National

    Park, Alberta, 1980-1983. Snow is measured in cm and

    usually occurred from October to April.   Accumulated snow

    is measured in cm (—).   Rainfall is measured in mm.   Snow

    accumulation data were available only from October, 1981

    to June 1983.

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1981

PRECIPITATION

TEMPERATURE (°C)

JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC

1982

PRECIPITATION

TEMPERATURE (°C)

JAN FEB MAR APR MAY JUN JUL AUG SEP OCT NOV DEC

1983
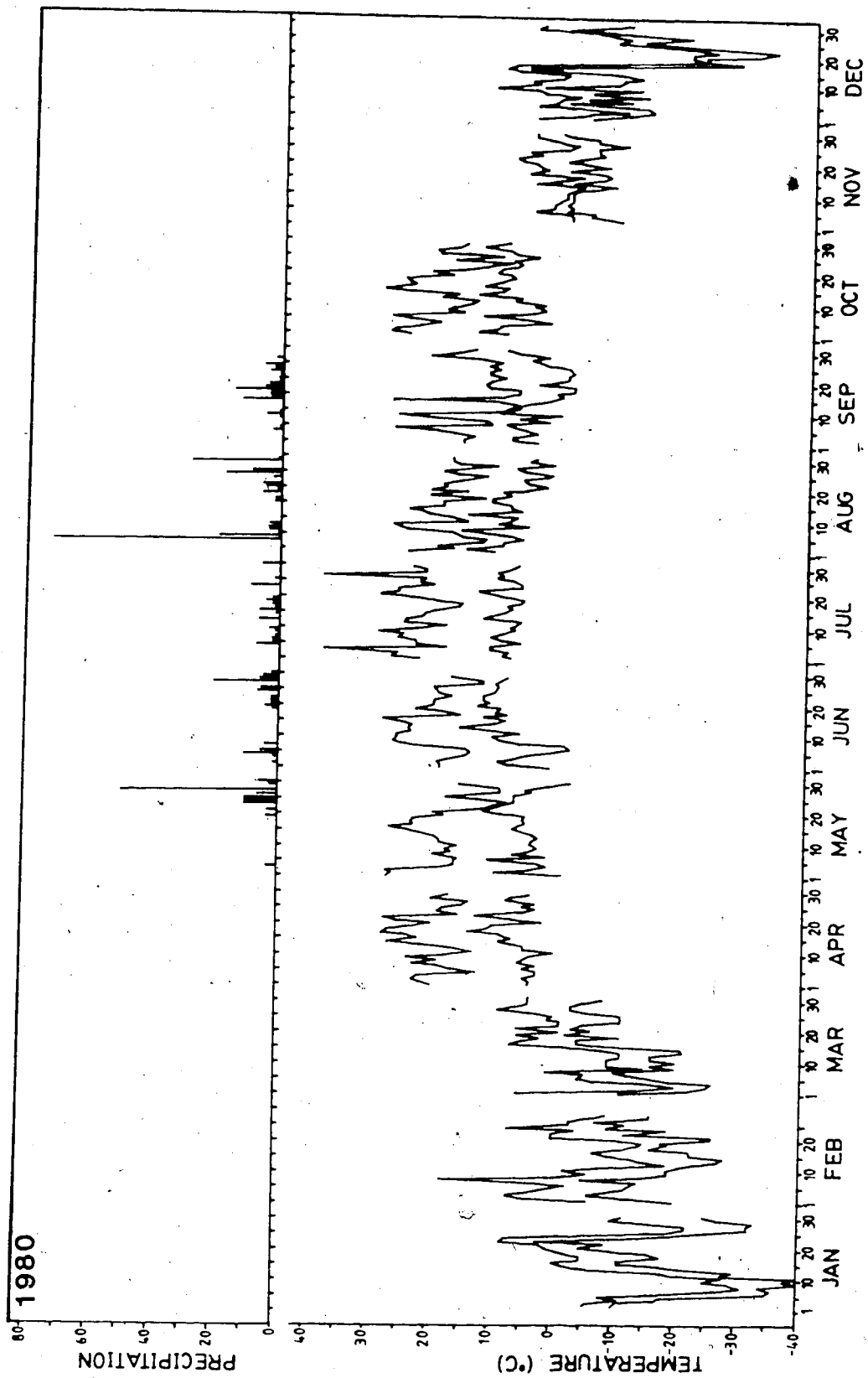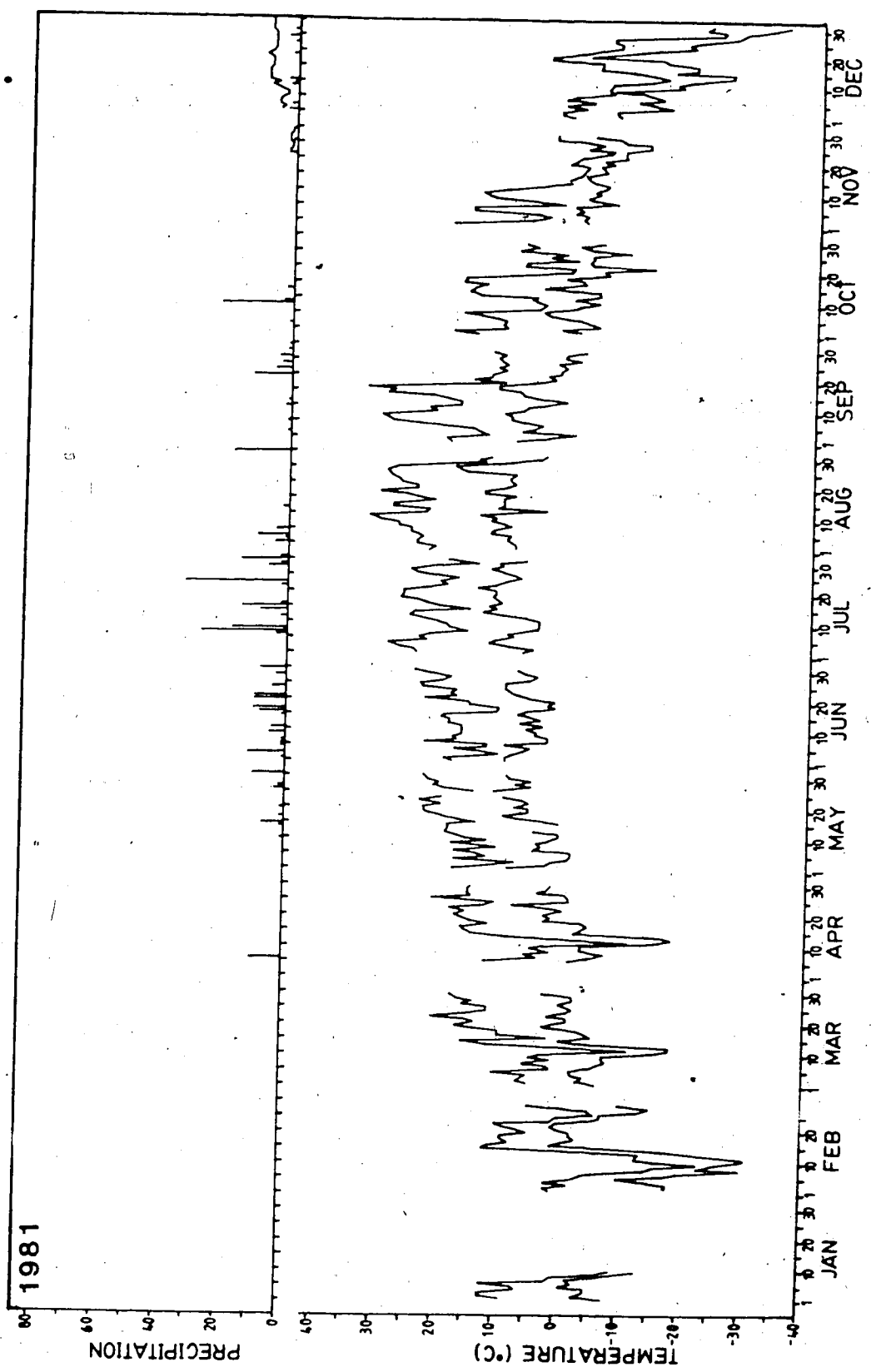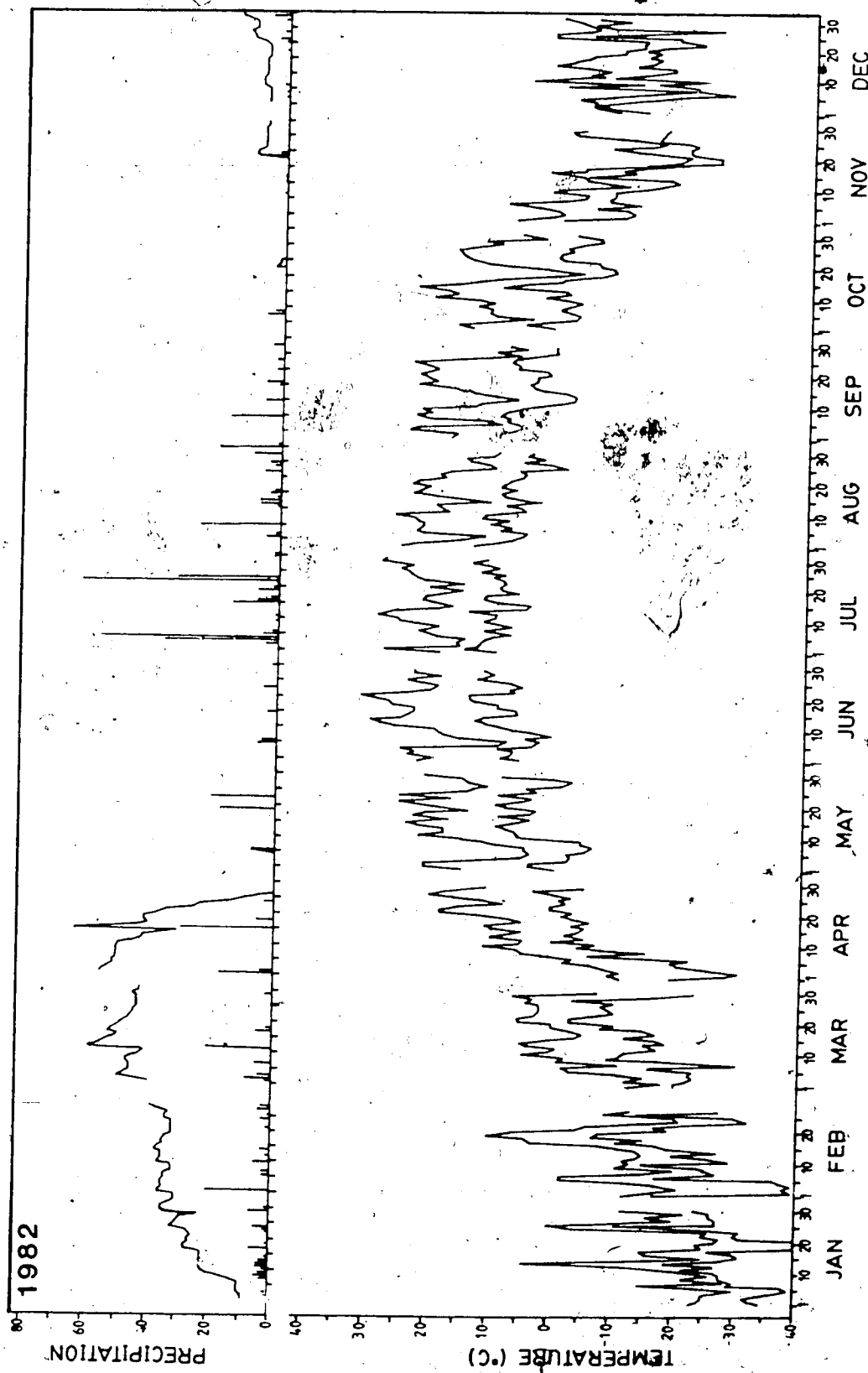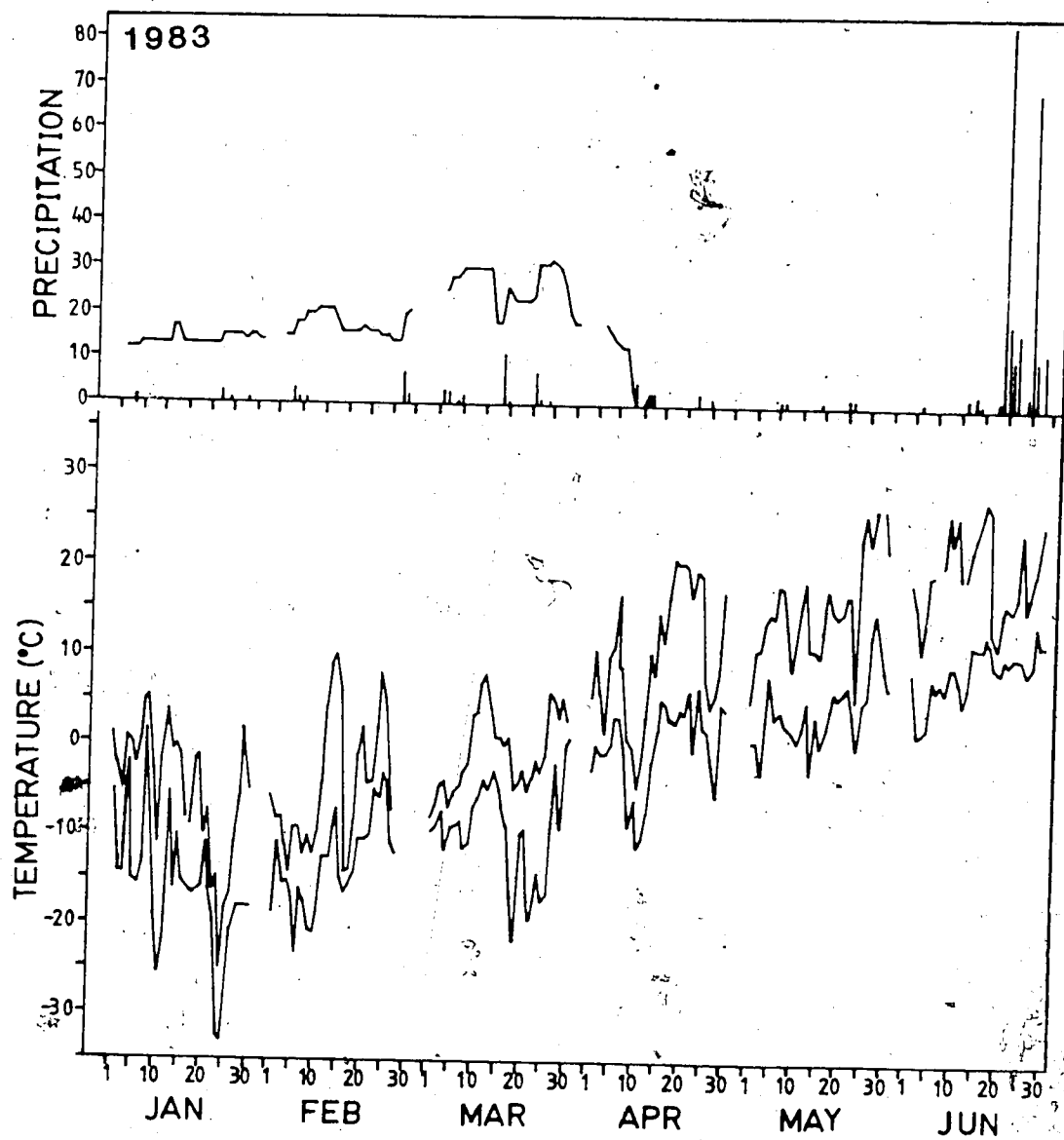
APPENDIX 3.   Annual trends in maximum and minimum temperatures and
relative humidity in three habitat types in Elk Island
National Park, Alberta, 1981 and 1982. a-aspen, b-bog,
g-grassland.

a 1981

b1981

g1981

a 1982

RELATIVE HUMIDITY (%)

TEMPERATURE (°C)

APR   MAY   JUN   JUL   AUG   SEP   OCT   NOV   DEC

b 1982

RELATIVE HUMIDITY(%)

TEMPERATURE (°C)

APR MAY JUN JUL AUG SEP OCT NOV DEC

g1982
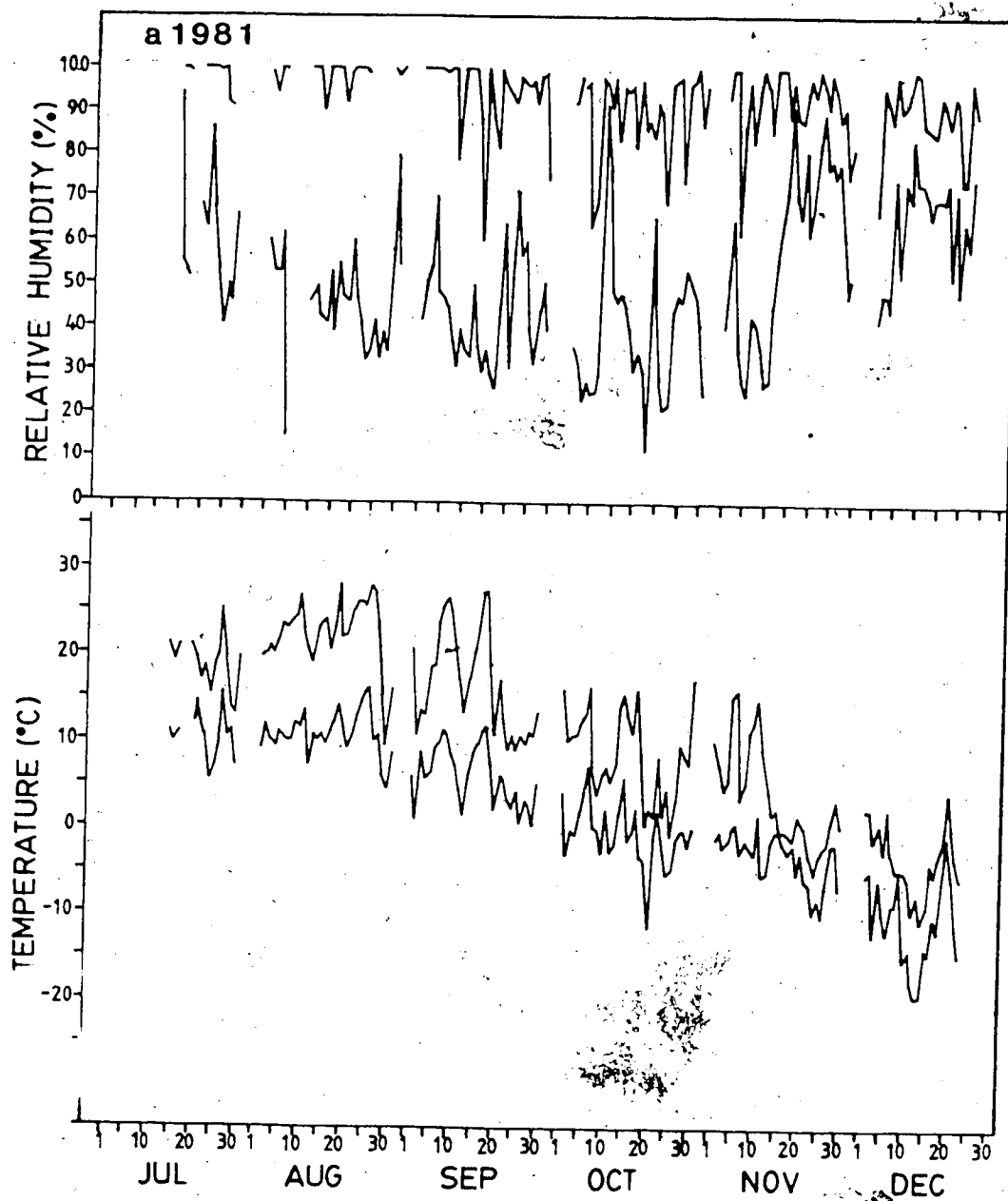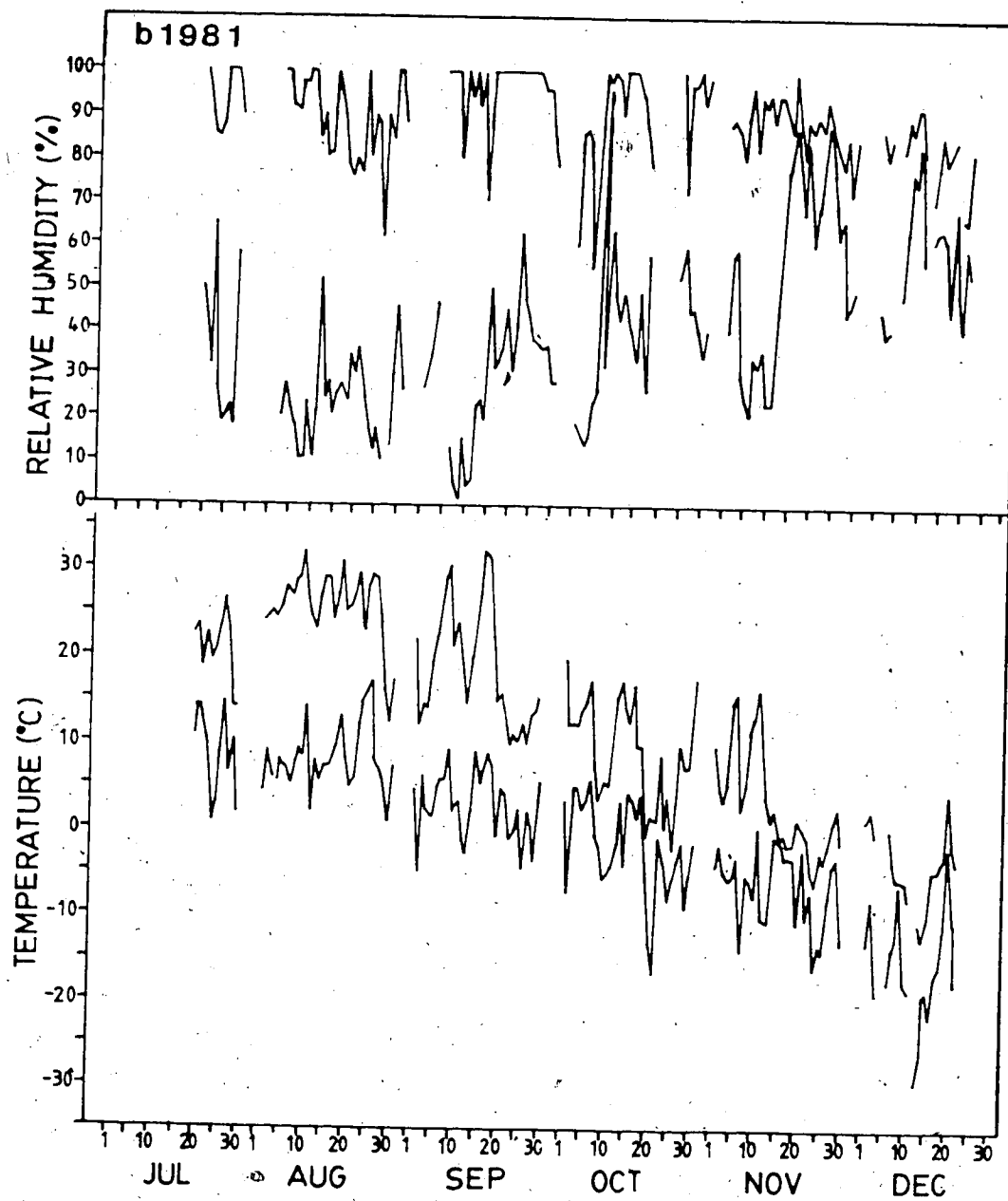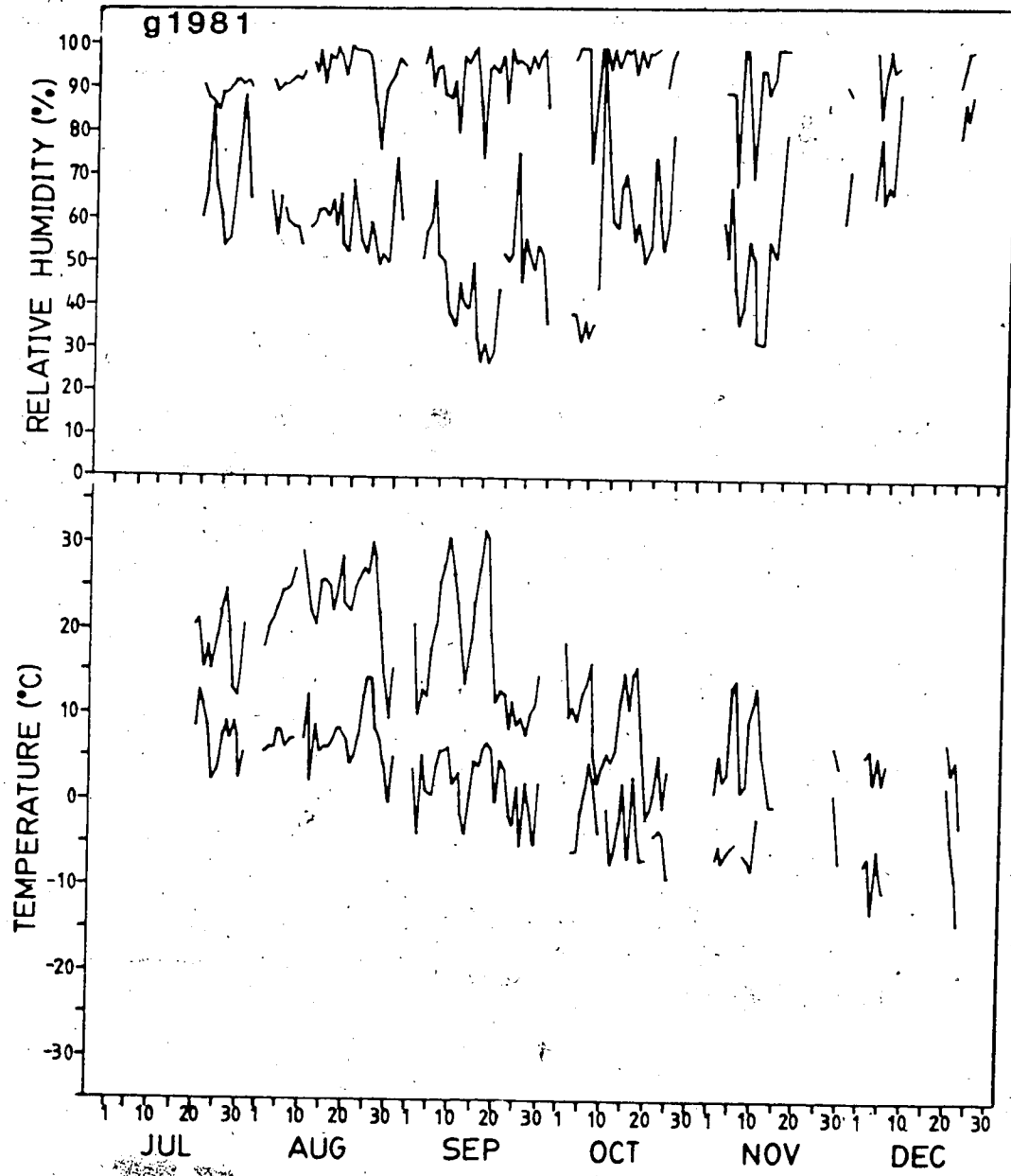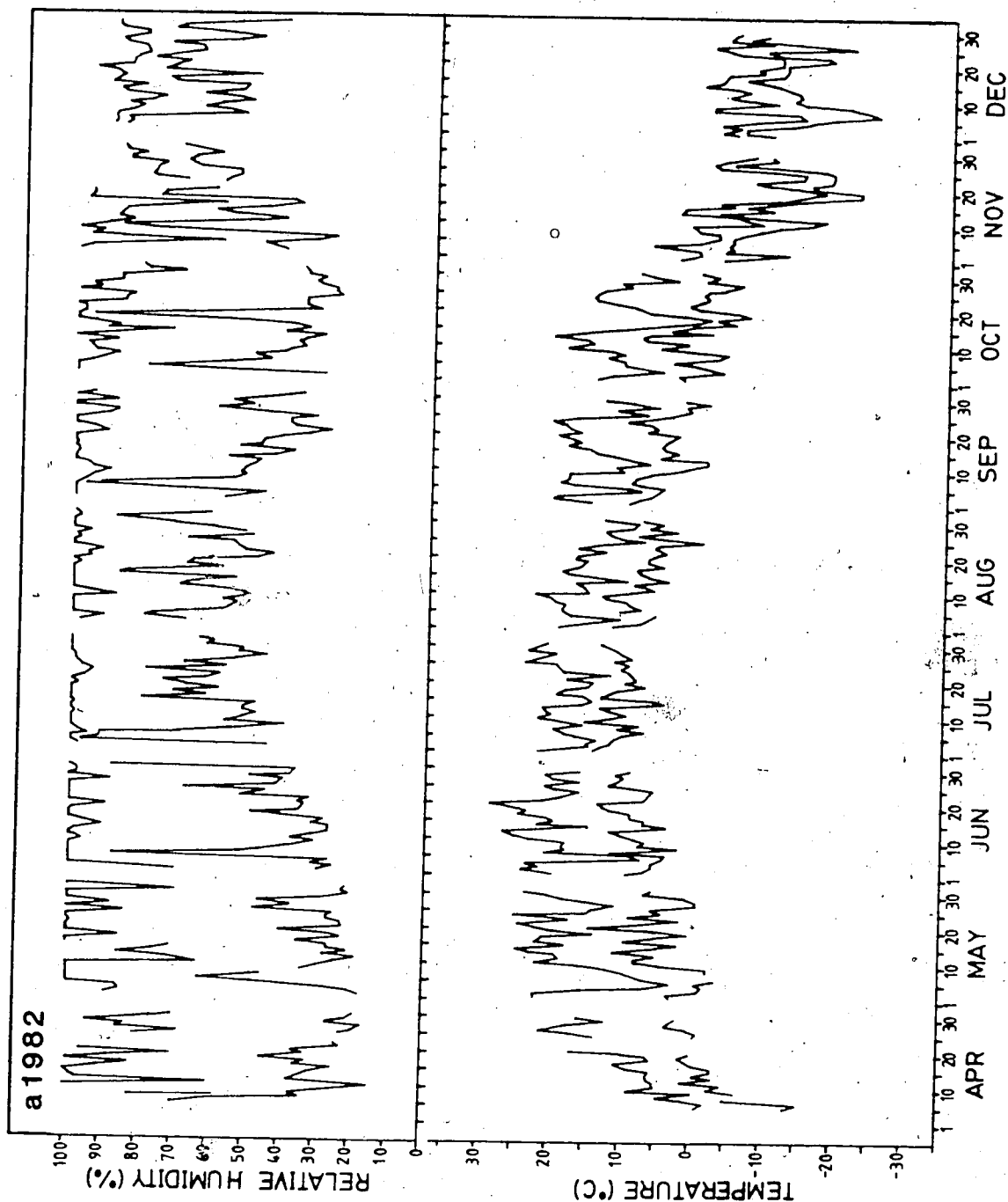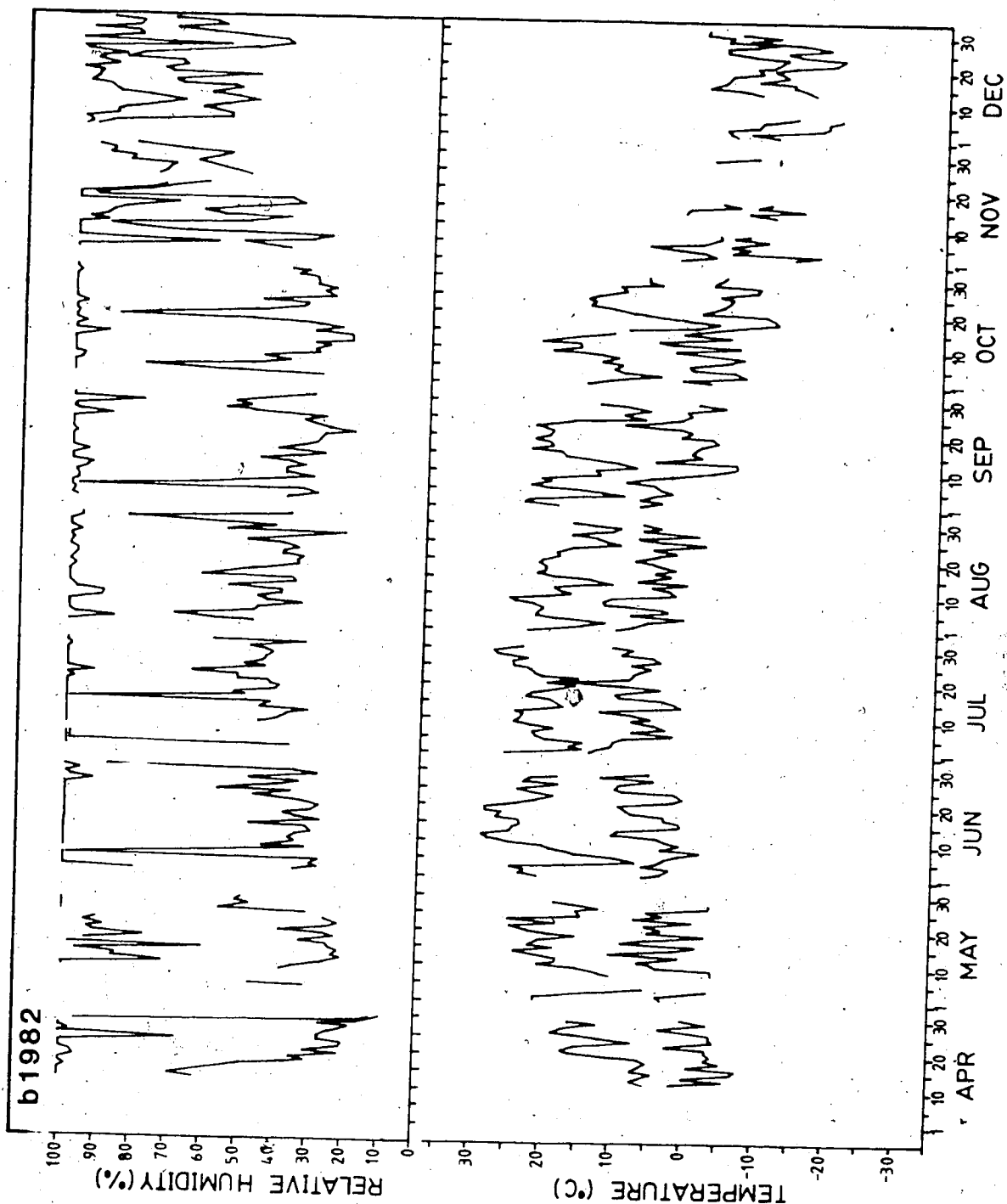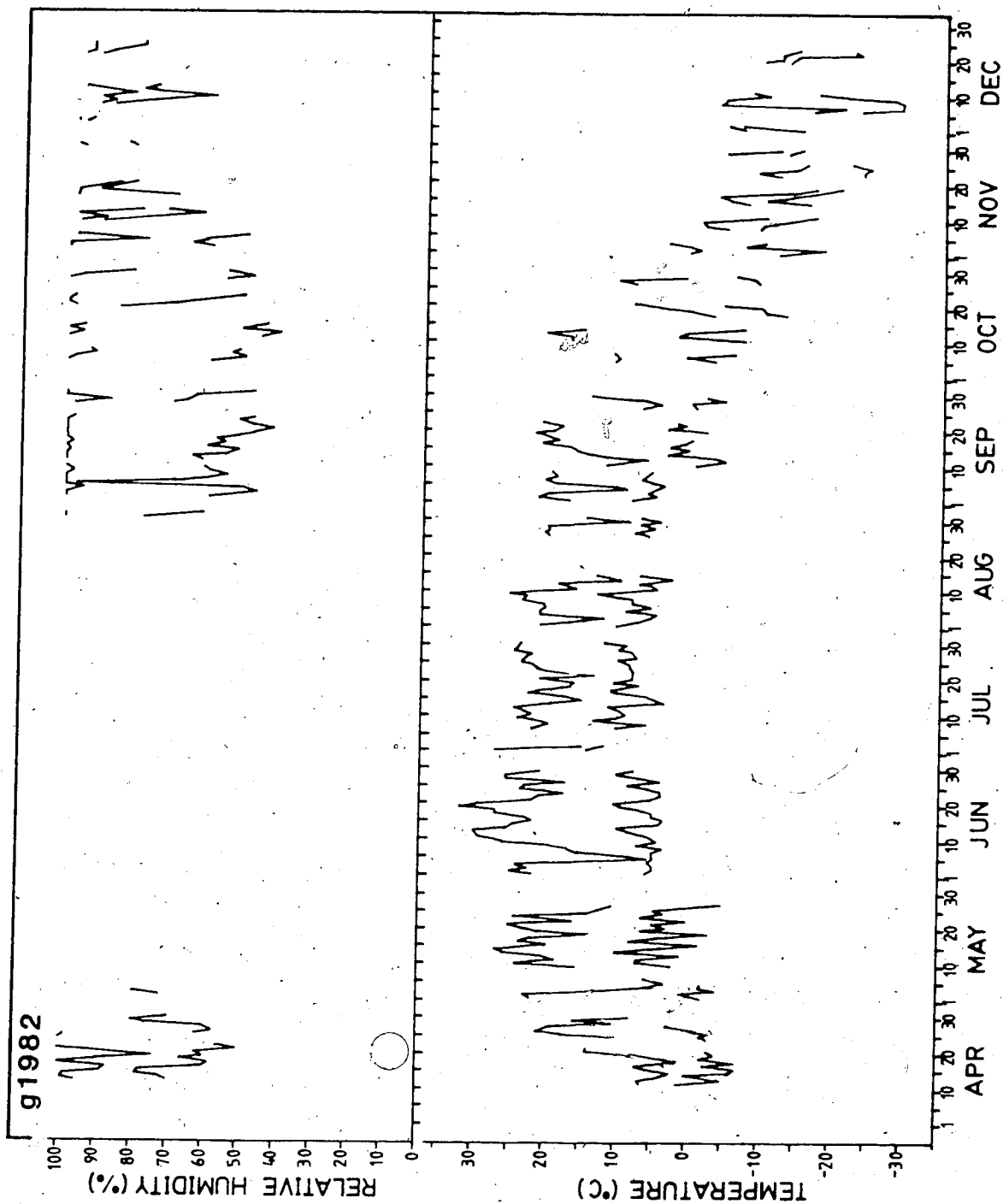
APPENDIX 4. Quantitative description of the canopy stratum at moose

carcass sites in Elk Island National Park, Alberta.

Carcass Site Number	Habitat Type	Tree Species	Relative Density	Relative Dominance	Relative Frequency	Importance Value
C1, C4, C6, C8, C15	Open canopy aspen	*Populus balsamifera*	42.0	49.2	38.7	129.9
		Populus tremuloides	33.3	32.6	34.7	100.6
		Betula papyrifera	17.4	5.3	18.7	41.1
		Picea glauca	7.5	12.9	8.0	28.4
C2, C14	Bog	*Picea mariana*	75.0	75.0	75.0	225.0
		Betula papyrifera	25.0	25.0	25.0	75.0
C3	Dense canopy mature aspen	*Populus tremuloides*	100.0	100.0	100.0	300.0
C5, C13	Grassland	—	—	—	—	—
C7	Dense canopy immature aspen	*Populus tremuloides*	68.8	82.7	57.1	208.6
		Populus balsamifera	31.3	17.3	42.9	91.5
C10, C11	Wet grassland/ sedge	*Populus balsamifera*	33.3	71.7	37.5	142.5
		Alnus spp.	60.0	19.7	50.0	129.7
		Picea mariana	6.7	8.6	12.5	27.8

Importance value is the sum of relative density, relative dominance and relative frequency to a maximum of 300.

APPENDIX 5.   Quantitative description of the shrub/herb strata at moose
carcass sites in Elk Island National Park, Alberta.

Carcass Site Number	Habitat Type	Vegetation Species	Relative Density	Relative Frequency	Importance Value
C1, C4, C6, C8, C15	Open canopy aspen	Maianthemum canadense	19.1	8.0	27.1
		Epilobium angustifolium	9.2	6.2	15.4
		Galium spp.	9.0	5.3	14.3
		Fragaria vesca	8.4	4.9	13.3
		Lathyrus ochroleucus	5.1	6.5	11.6
		Rosa acicularis	5.3	6.1	11.4
		Symphoricarpos albus	3.2	7.1	10.3
		Graminae	2.2	8.0	10.2
		Rubus spp. (Blackberry)	4.2	5.7	9.9
		Viola spp.	3.9	5.4	9.3
		Equisetum spp.	5.5	3.7	9.2
		Corylus cornuta	5.5	3.5	9.0
		Rubus spp. (Raspberry)	3.2	3.7	6.9
		Aralia nudicaulis	2.0	2.7	4.7
		Lysimachia ciliata	2.3	2.4	4.7
		Populus tremuloides	1.1	3.3	4.4
		Populus balsamifera	1.5	2.9	4.4
		Ribes hudsoniasnum	0.7	2.8	3.5
		Lonicera involucrata	1.2	1.9	3.1
		Similax glauca	0.5	1.8	2.3
		Amelanchier alnifolia	0.7	1.4	2.1
		Ribes spp.	0.3	1.2	1.5
		Similacina trifolia	0.5	1.0	1.5
		Cornus alternifolia	0.2	1.0	1.2
		Parthenocissus spp.	0.2	1.0	1.2
		Salix spp.	0.3	0.4	0.7
		Cornus stolonifera	0.1	0.4	0.5
C2, C14	Bog	Spagnum spp.	44.9	23.4	68.3
		Ledum groenlandicum	27.2	23.4	50.6
		Vaccinium macrocarpon	14.8	23.4	38.2
		Cladonia rangiferina	3.6	10.0	13.6
		Rubus chamaemorus	4.5	9.0	13.5
		Vaccinium spp.	2.9	6.0	8.9
		Betula papyrifera	1.2	2.5	3.7
		Picea mariana	1.2	2.5	3.7
C3	Dense canopy mature aspen	Aralia nudicaulis	11.9	7.3	19.2
		Rubus spp. (Blackberry)	9.9	7.3	17.2
		Viola spp.	13.5	3.6	17.1
		Epilobium angustifolium	9.0	7.3	16.3
		Lathyrus ochroleucus	7.9	7.3	15.2
		Galium spp.	9.4	5.5	14.9
		Rosa acicularis	5.8	7.3	13.1
		Ribes spp.	4.9	5.5	10.4
		Smilax glauca	4.9	5.5	10.4
		Graminae	1.6	7.3	8.9
		Ribes hudsonianum	2.9	5.5	8.4
		Populus tremuloides	2.5	5.5	8.0
		Solidago spp.	4.0	3.6	7.6
		Rubus spp. (Raspberry)	1.6	5.5	7.1

Carcass Site Number	Habitat Type	Vegetation Species	Relative Density	Relative Frequency	Importance Value
C3 ...cont'd		Lonicera involucrata	2.5	3.6	6.1
		Maianthemum canadense	3.4	1.8	5.2
		Corylus cornuta	0.5	1.8	2.3
		Equisetum spp.	0.5	1.8	2.3
		Mertensia virginica	0.5	1.8	2.3
		Parthenocissus spp.	0.5	1.8	2.3
		Symphoricarpus albus	0.5	1.8	2.3
C5, C13	Grass-land	Equisetum spp.	33.4	15.0	48.4
		Graminae	12.9	28.6	41.5
		Populus tremuloides	7.2	16.6	23.8
		Rosa acicularis	9.9	11.6	21.5
		Fragaria vesca	12.2	8.6	20.8
		Solidago spp.	10.9	4.6	15.5
		Symphoricarpos albus	8.8	6.6	15.4
		Galium spp.	3.6	4.6	8.2
		Rubus spp. (Blackberry)	1.1	2.0	3.1
		Lonicera involucrata	0.3	2.0	2.3
C7	Dense canopy immature aspen	Equisetum spp.	39.8	10.8	50.6
		Fragaria vesca	23.9	10.8	34.7
		Symphoricarpos albus	7.2	10.8	18.0
		Rubus spp. (Raspberry)	6.8	10.8	17.6
		Lysimachia ciliata	7.9	8.8	16.7
		Viola spp.	5.4	8.8	14.2
		Graminae	1.3	8.8	10.1
		Galium spp.	2.5	5.9	8.4
		Ribes spp.	2.1	5.9	8.0
		Populus tremuloides	1.3	5.9	7.2
		Smilax glauca	0.4	3.9	4.3
		Aralia nudicaula	0.4	2.9	3.3
		Epilobium angustifloium	0.4	2.9	3.3
		Rosa acicularis	0.4	2.9	3.3
C10, C11	Wet grass-land/ sedge	Equisetum spp.	53.7	13.8	67.5
		Graminae/Carex spp.	7.8	19.4	27.2
		Viola spp.	5.5	10.0	15.5
		Epilobium angustifolium	6.1	7.6	13.7
		Unknown #1	6.7	3.4	10.1
		Rubus spp. (Raspberry)	2.3	7.6	9.9
		Rosa acicularis	1.9	7.6	9.5
		Salix spp.	1.9	5.3	7.2
		Lonicera involucrata	4.6	1.9	6.5
		Ribes spp.	2.0	4.3	6.3
		Rubus spp. (Blackberry)	2.0	4.3	6.3
		Aralia nudicaulis	0.9	4.3	5.2
		Betula glandulosa	1.7	3.4	5.1
		Populus balsamifera	1.3	1.9	3.2
		Ribes hudsoniasnum	0.9	1.9	2.8
		Smilax glauca	0.7	1.9	2.6
		Lysimachia ciliata	0.4	1.9	2.3

Importance value is the sum of relative density and relative frequency to a maximum of 200.

APPENDIX 6. Sampling for larval <u>Dermacentor albipictus</u>; means and standard deviations.

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Date	Carcass Flagging		Flannel Squares	Trail Flagging	
	1981	1982[a]	1981	1981	1982
8/27	----	0	----	----	0
9/6	----	110	----	----	0.8 ± 1
9/13	----	395	----	----	0.2 ± 0.4
9/14	172 ± 454[b]	----	0	----	----
9/20	----	295	----	----	0.5 ± 0.6
9/21	1729 ± 3623	----	210 ± 408	----	----
9/27	1615 ± 3366	362	370 ± 447	73 ± 130	0.8 ± 2
10/4	6971 ± 11965	90	1055 ± 2134	58 ± 90	0.5 ± 0.8
10/11	4246 ± 8045	207	521 ± 1026	45 ± 44	0.8 ± 0.8
10/18	4669 ± 8780	42	440 ± 855	48 ± 45	1 ± 1
10/25	3294 ± 6759	155	372 ± 779	25 ± 23	1 ± 1
11/1	3845 ± 7498	55	304 ± 627	42 ± 56	0.3 ± 0.5
11/8	1734 ± 3206	9	96 ± 177	12 ± 12	0
11/15	1915 ± 3831	15	73 ± 116	17 ± 17	0.2 ± 0.4
11/22	634 ± 1097	1	53 ± 107	6 ± 10	0.3 ± 0.5
11/29	191 ± 319	2	38 ± 64	7 ± 15	0
12/6	237 ± 495	0	8 ± 7	0.5 ± 0.8	0
12/13	6 ± 6	0	3 ± 5	0.2 ± 0.4	0
12/20	9 ± 13	0	----	0.3 ± 0.5	0
12/24	1 ± 1	----	----	----	----

[a] Larvae were recovered from only 1 carcass.

[b] mean $\pm$ 1 SD.

APPENDIX 7. Summaries of weekly counts of instars of <u>Dermacentor</u>

<u>albipictus</u> on experimentally infested moose, 1981-82 and

1982-83. O = larvae, ● = engorged larvae, □ = nymphs,

■ = engorged nymphs, ☆ = males, △ = females, ▲ = engorged

females.

M046   PRE-ADULT

ADULT

TICKS COUNTED   (%)

SEP   OCT   NOV   DEC   JAN   FEB   MAR   APR   MAY

MO59 PRE-ADULT

ADULT

MO 60 PRE-ADULT

TICKS COUNTED (%)

100 90 80 70 60 50 40 30 20 10 0

20 30 10 20 30 9 19 29 9 19 29 8 18 28 7 17 27 9 19 29 9 19 27 8 18 28 7 17 27
SEP   OCT   NOV   DEC   JAN   FEB   MAR   APR MAY

M068 PRE-ADULT

ADULT

M069 PRE-ADULT

ADULT

TICKS COUNTED (%)

SEP OCT NOV DEC JAN FEB MAR. APR MAY

MO 50 PRE-ADULT

ADULT

MO55 PRE-ADULT

TICKS COUNTED (%)

SEP OCT NOV DEC JAN FEB MAR APR MAY
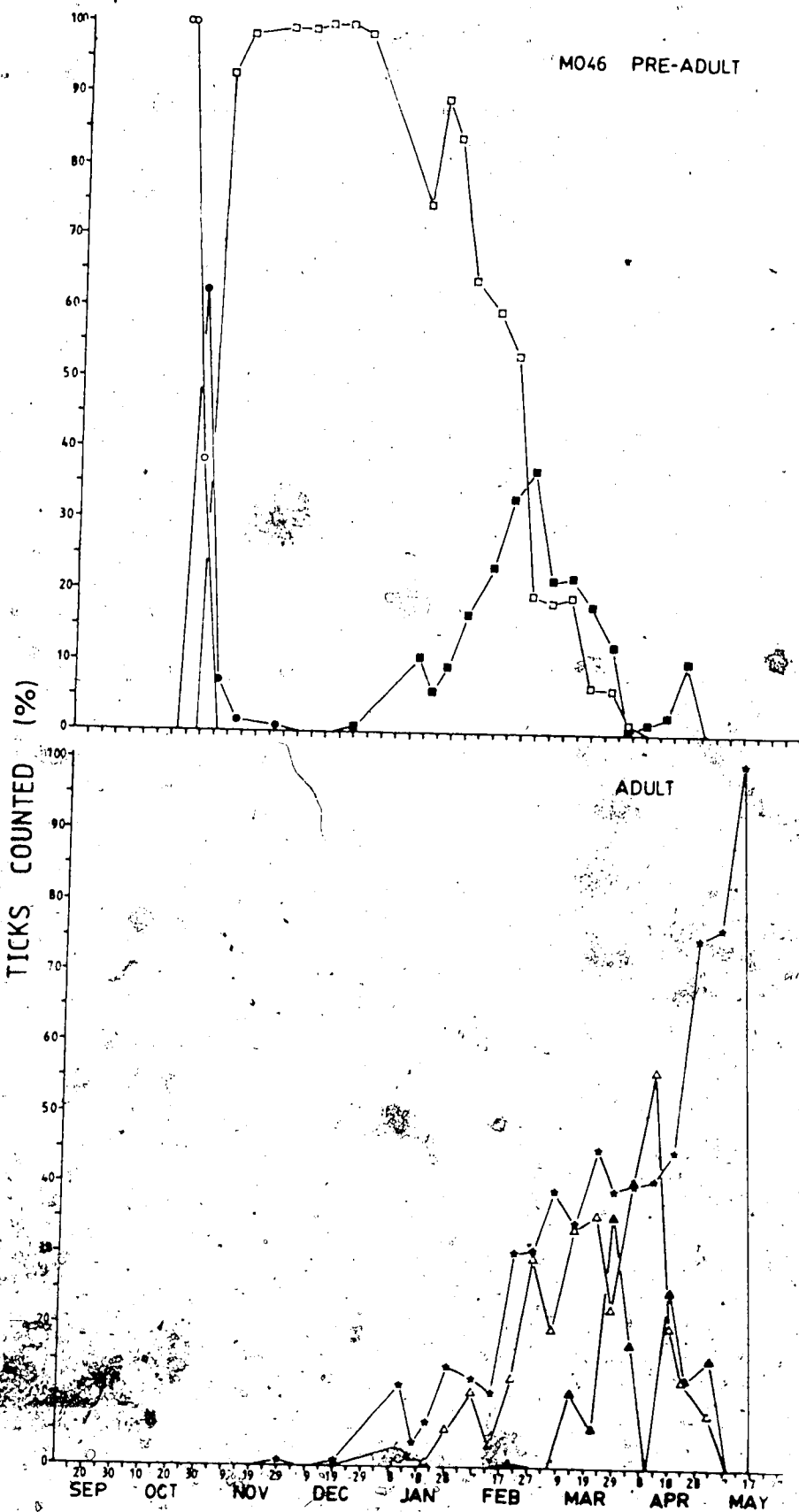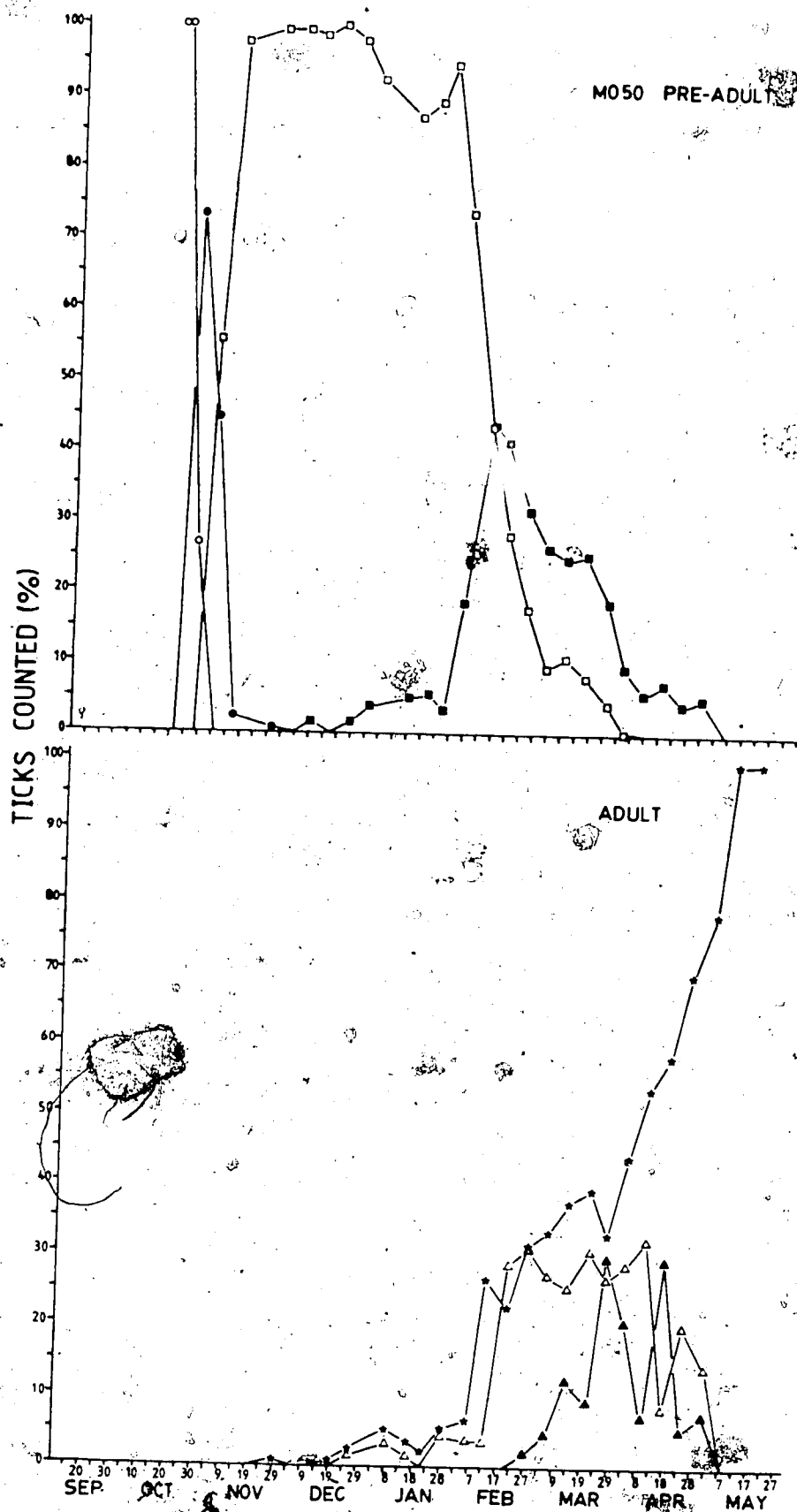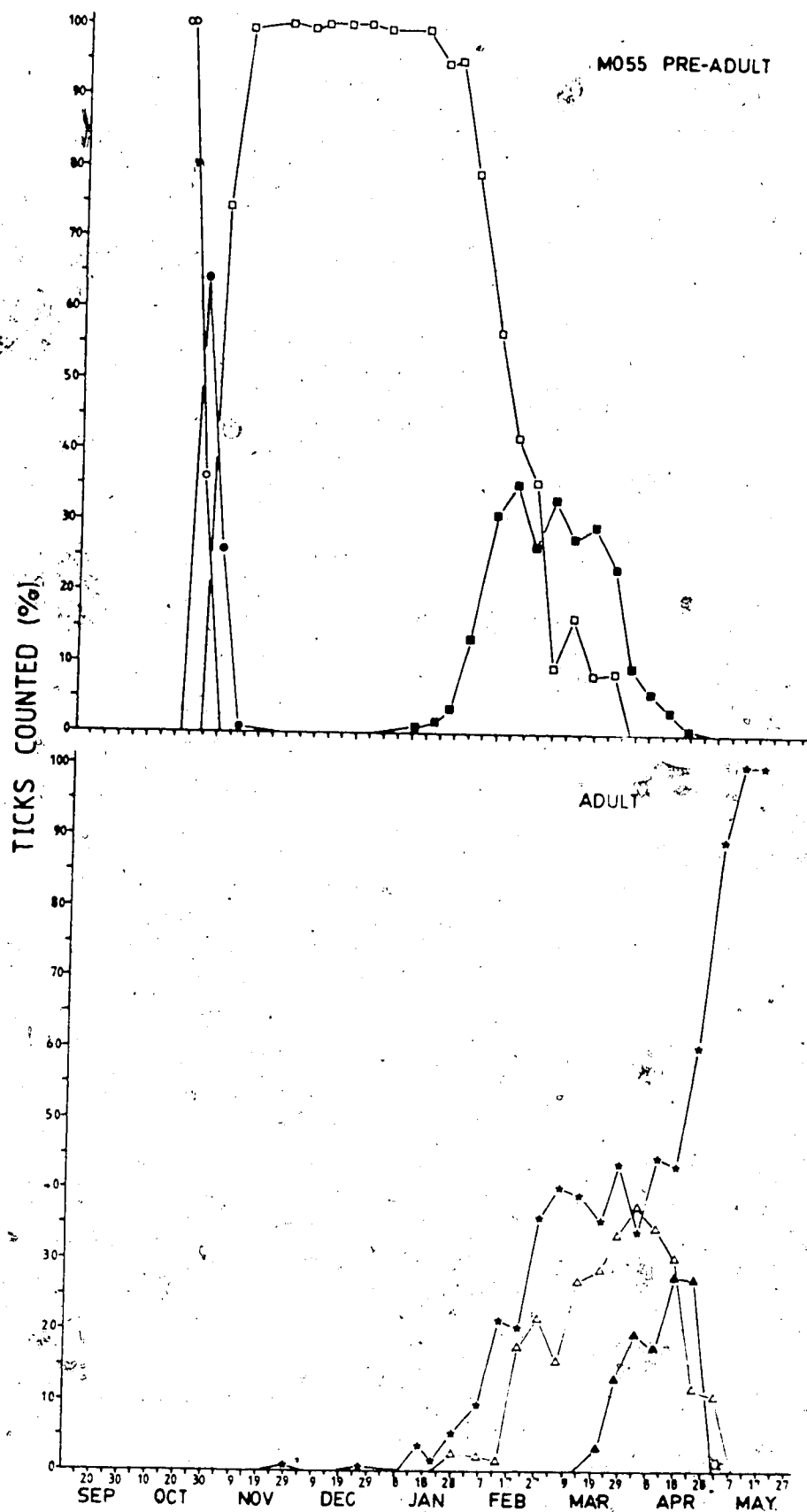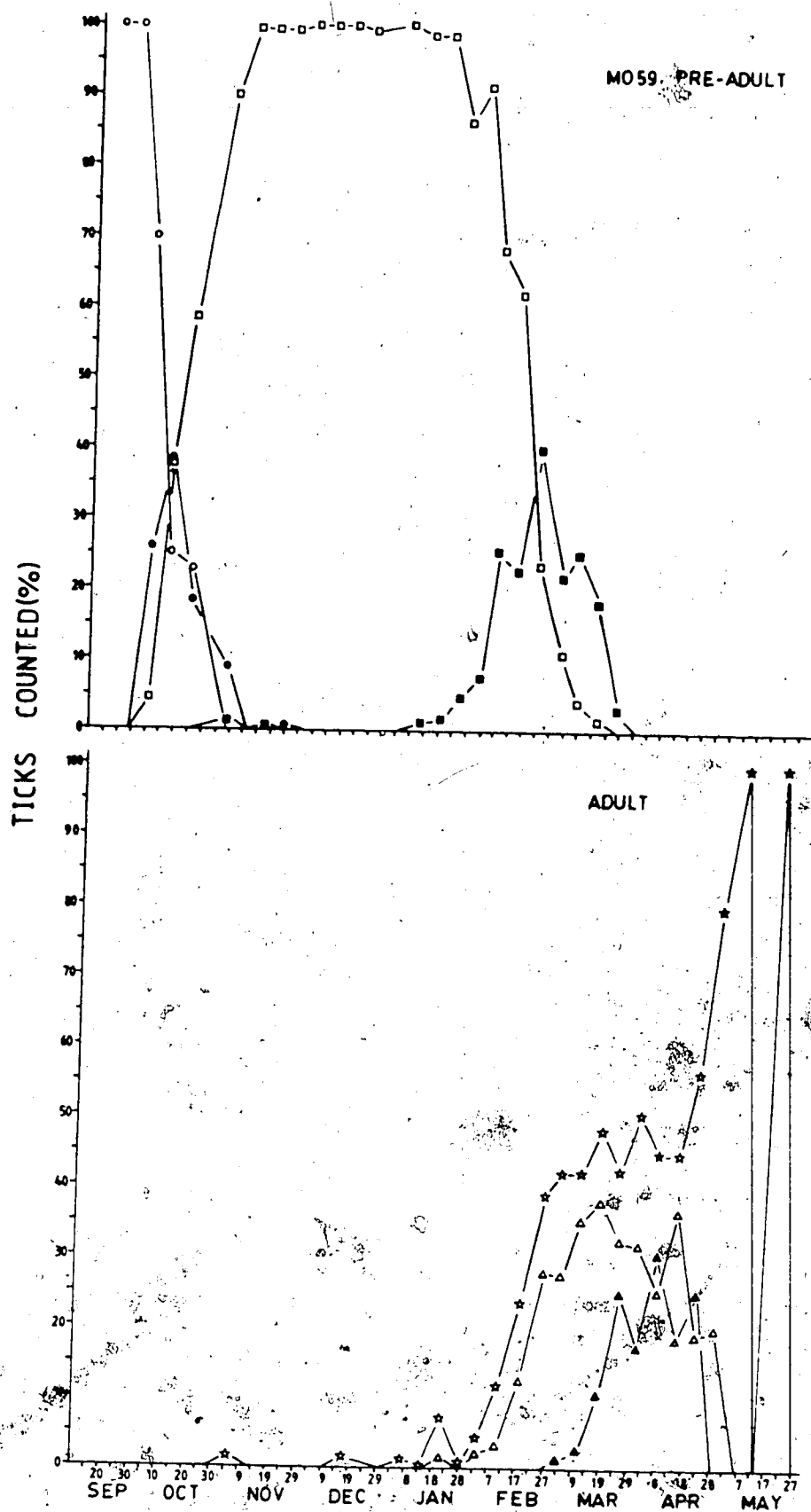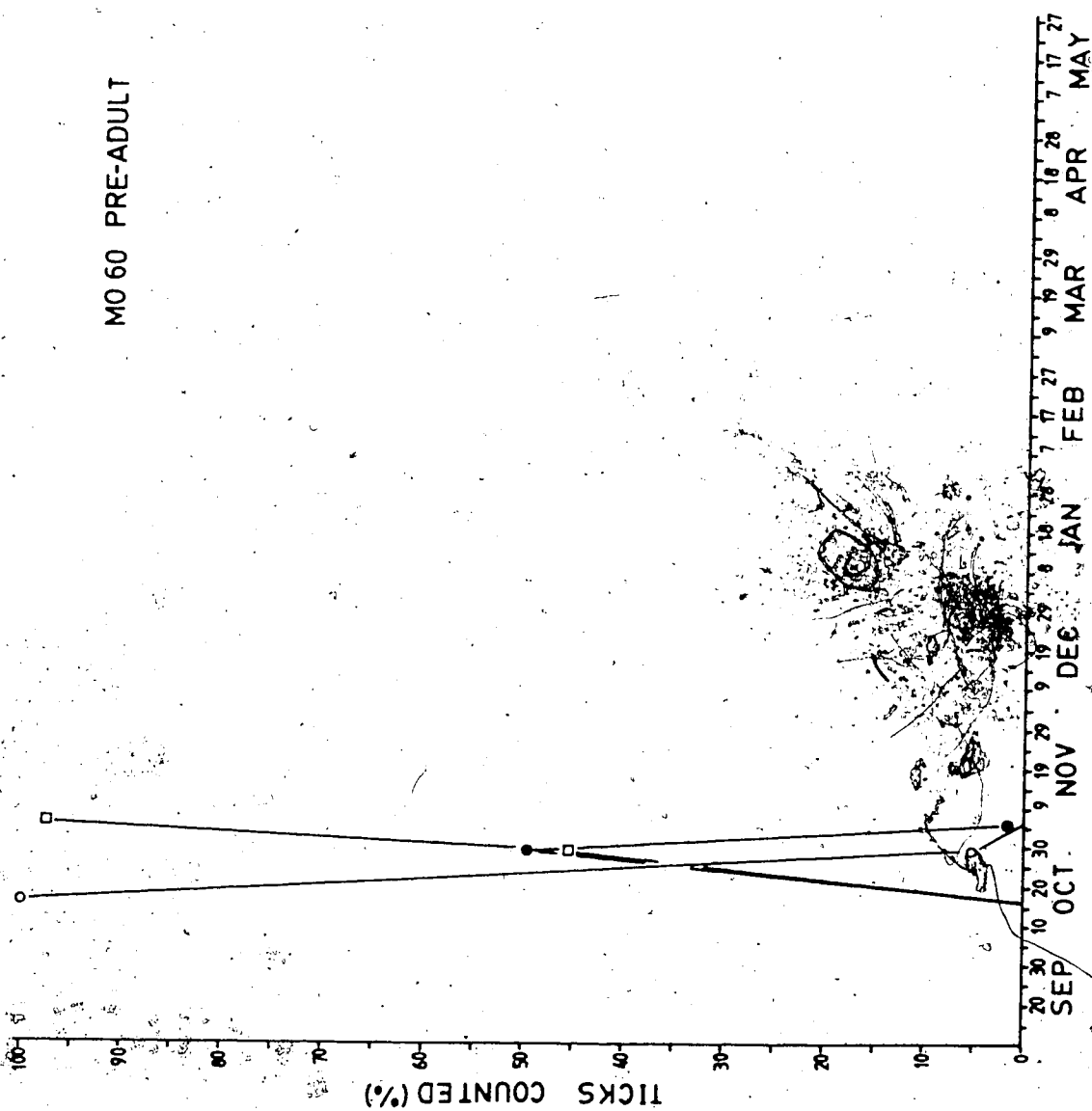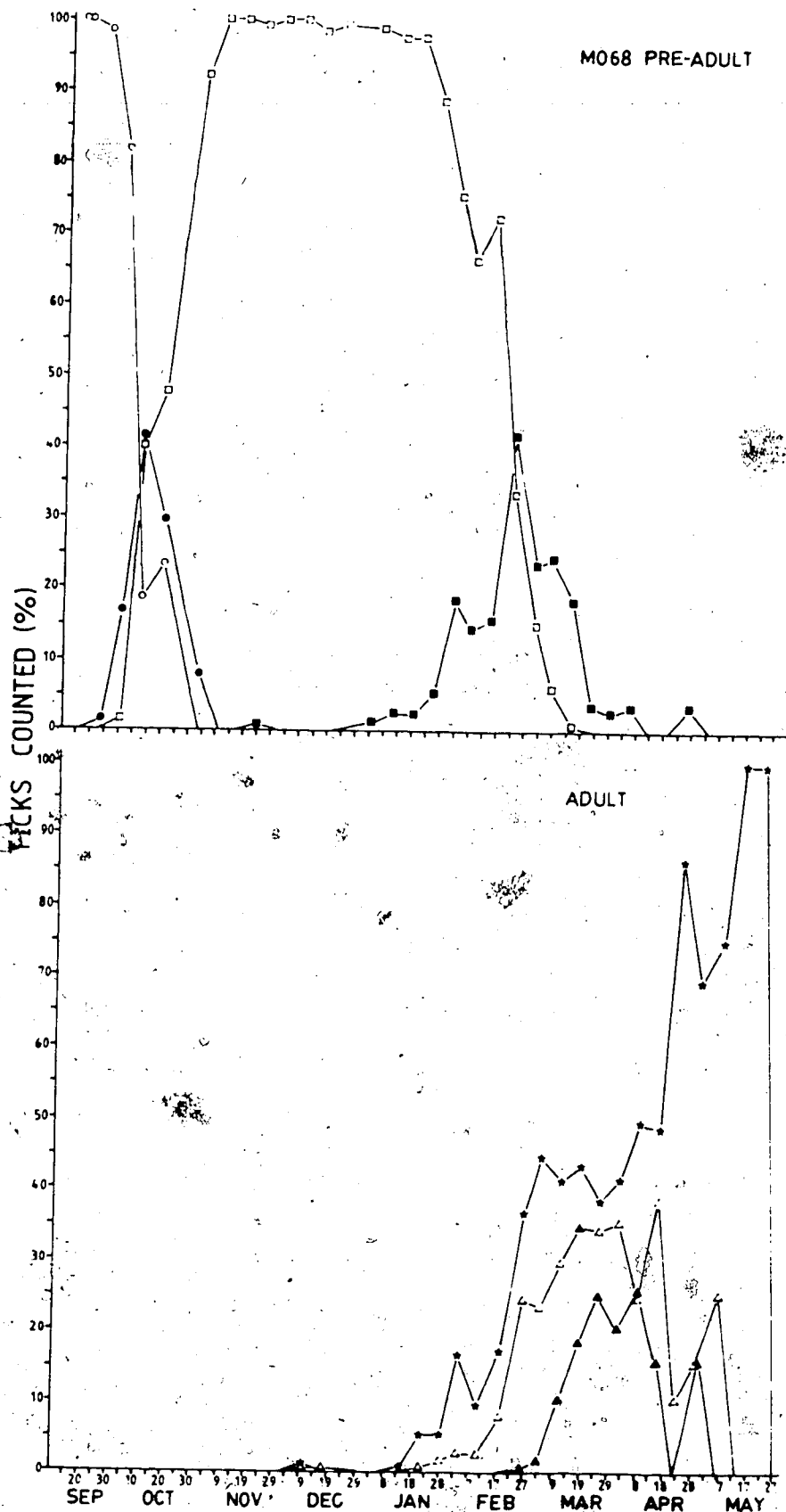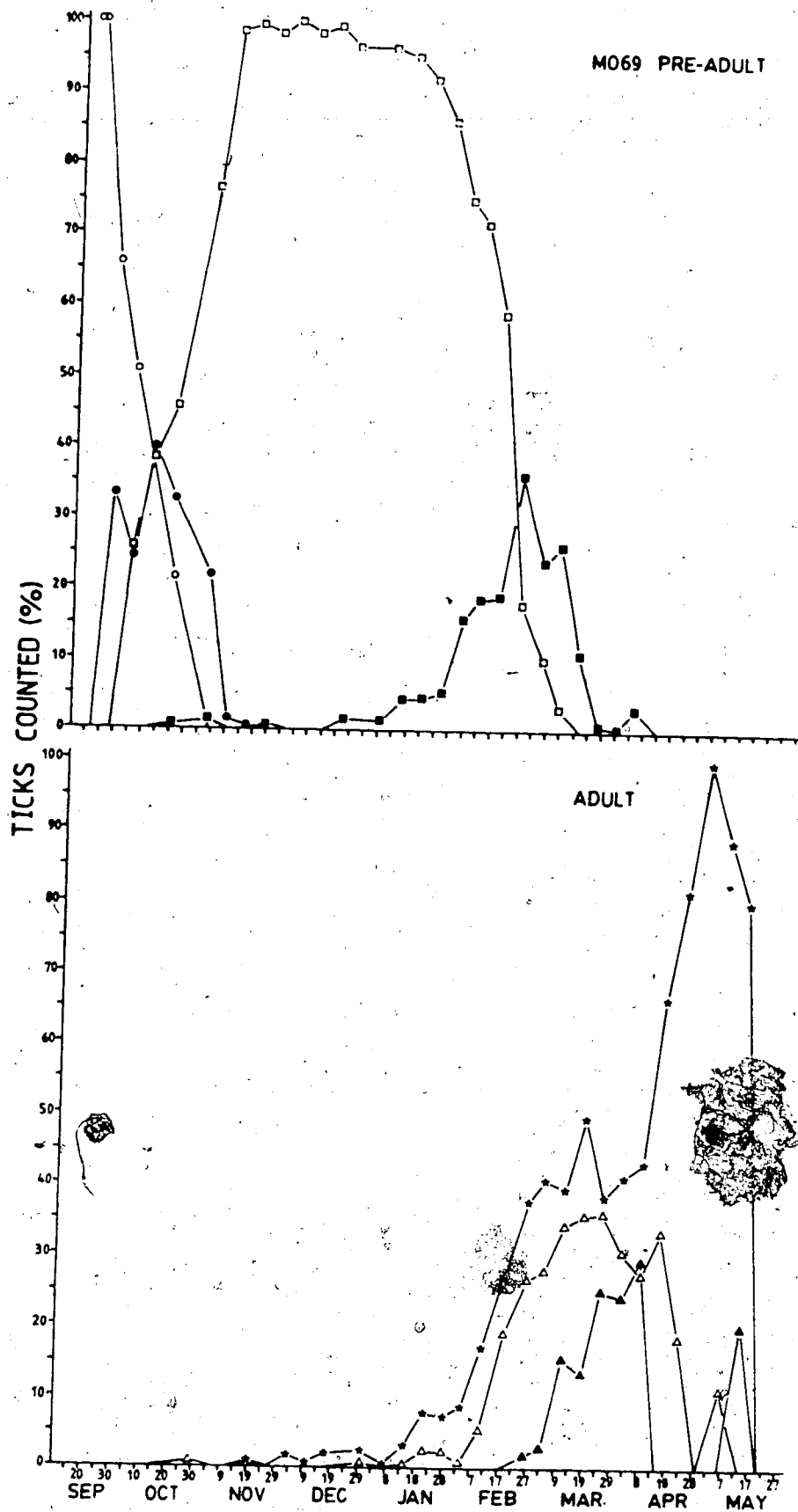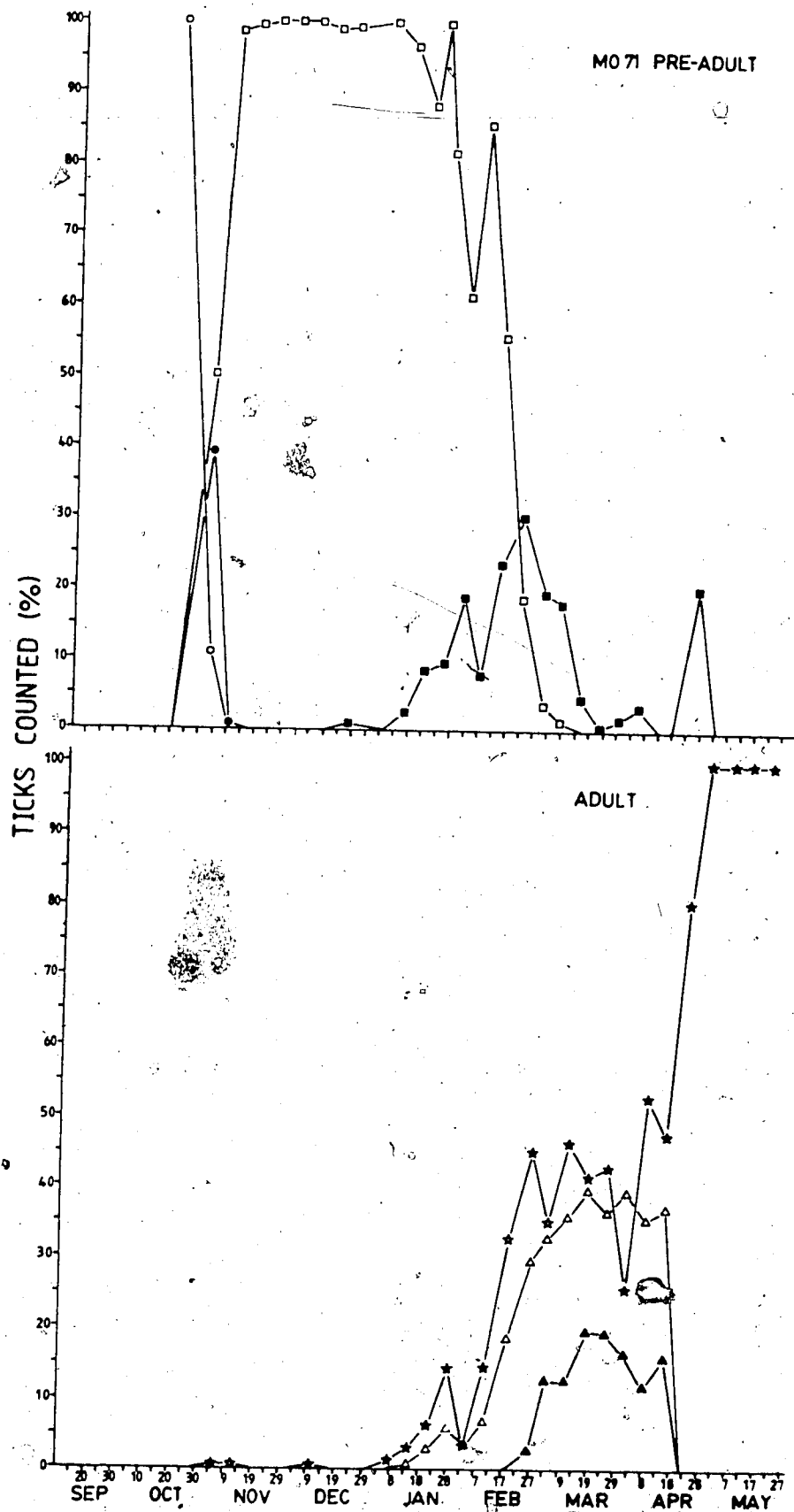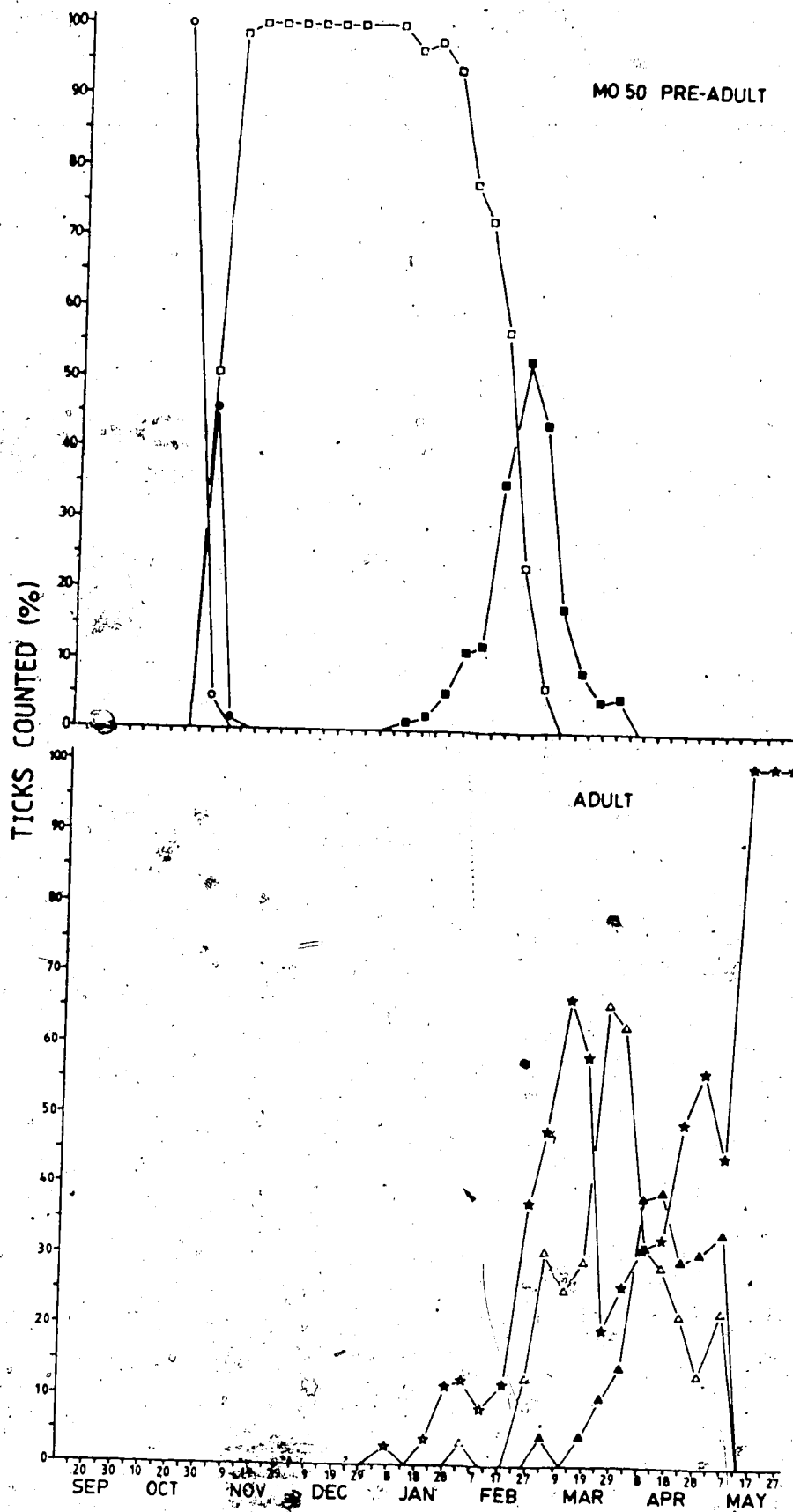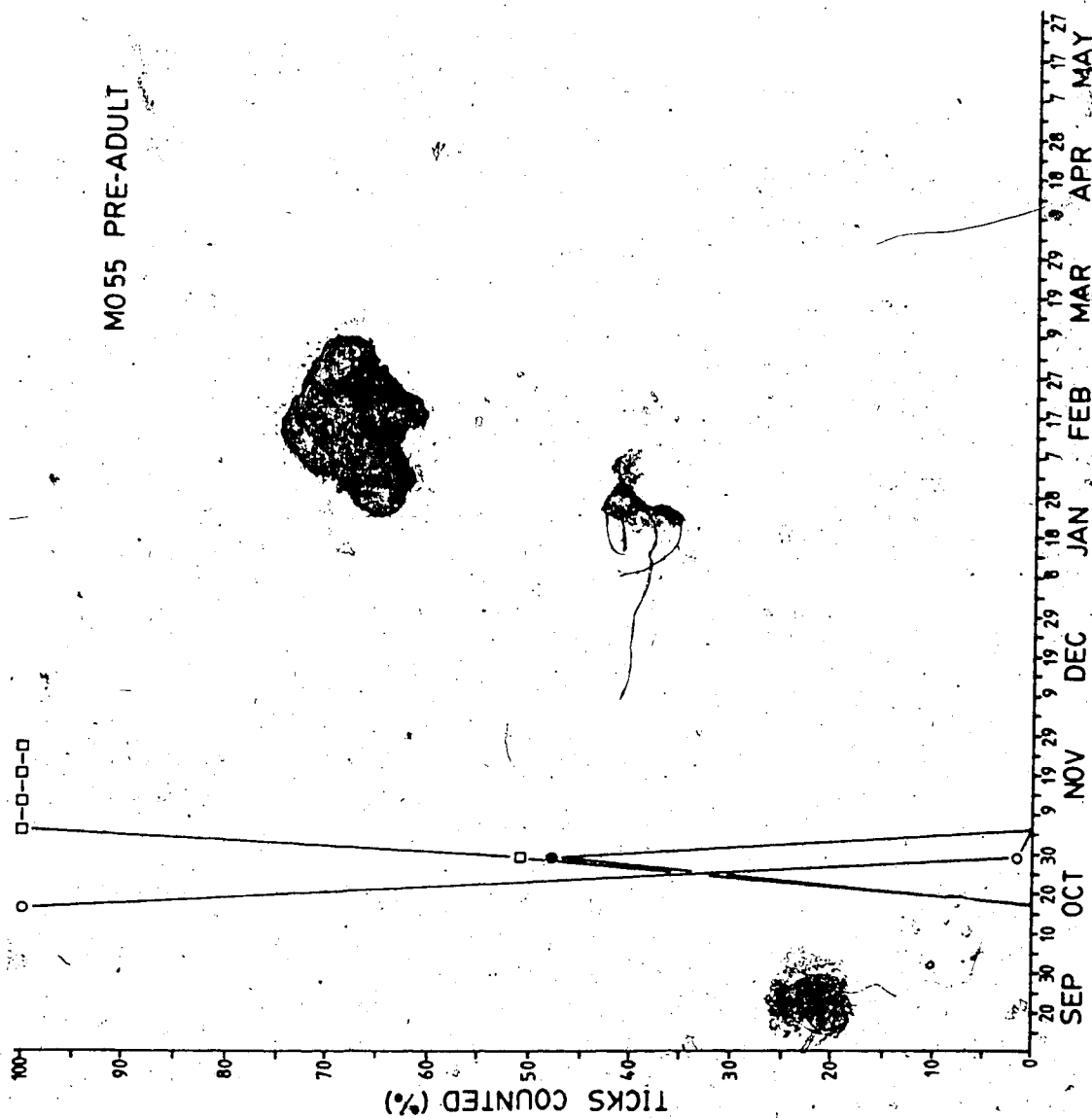
APPENDIX 8. Reproductive parameters of engorged female Dermacentor

albipictus under experimental conditions, 1982 and 1983.

The reproductive performance of engorged female (EF) ticks is normally measured under constant temperature and relative humidity in the laboratory. A variety of incubation conditions were used, the results of these experiments are presented here.

The most important reproductive parameters monitored in this study were EF survival, preoviposition and incubation periods, total production, % egg hatch, % larval survival, and the Reproductive Efficiency Index (REI). Although many of the reproductive parameters were relatively constant between experimental replicates within a treatment group, important variations and trends in these parameters are identified within each treatment group. Because EF that laid unsuccessful eggs constituted a variable proportion of the total number of EF used in each experiment, an anaysis of the reproductive performance of these EF is included in the discussion of the results within each treatment group where applicable.

Reproduction of engorged females under field conditions at Elk Island National Park

The reproductive parameters of succesful EF under field conditions as discussed previously. Twenty-six EF, over half of which were in the aspen habitat, laid eggs that failed to hatch (Table 1). The preoviposition period of these EF was not different in the three habitat types (F=.0526, .0894, .3581, p=.8192, .7657, .5512 for the bog, aspen, and grassland, respectively) or from succesful EF (F=.4819, p=.7900). Total production and REI were similar between habitat types, but total production was significantly less in the bog and grassland for unsuccessful EF than for successful EF (F=7.248, 7.356, p=.0086, .0081, respectively). The REI showed the same relationships as total production (F=10.505, 11.970, p=.0077, .0009, respectively).

Reproduction of engorged females at constant conditions

Sixty and 72% of the EF at 25°C and 19°C, respectively, survived and laid successful eggs (Tables 2 and 3). There was little change in EF survival over time at 25°C except for 22 May. Survival of EF at 19°C increased with successive drop periods.

All reproductive parameters except preoviposition period, which declined over time, were reasonably similar between drop periods for both 25°C and 19°C (Tables 2 and 3). The preoviposition period at 25°C was correlated with date the experiment began

Table 1. Reproductive parameters of engorged female (EF) *Dermacentor albipcitus* under field conditions in three habitat types in Elk Island National Park, Alberta, 1982.

Site	No. of EF	EF Survival No.[a]	EF Survival %	Preoviposition (days)	Incubation (days)	Total Production (eggs/EF)	Percent of Eggs that Hatch (95% CI)[b]	Percent of Larvae that Survive (95% CI)[b]	Reproductive Efficiency Index (eggs/g EF)
Successful females[c]									
BOG	74	25	34	40.6 ± 16.8*	81.4 ± 11.8	3227 ± 1590	51(39, 62)	14(6, ?6)	6029 ± 1773
ASPEN	78	10	13	39.2 ± 18.6	105.9 ± 21.3^{d}	3013 ± 1319	23(9, 41)	6(1, 18)	5579 ± 2119
GRASSLAND	73	27	37	36.2 ± 15.3	79.4 ± 9.6	3152 ± 1361	59(44, 72)	36(21, 51)	5897 ± 2179
Unsuccessful females[c]									
BOG	74	5	7	45.8 ± 22.4	---	1400 ± 964	---	---	874 ± 1694^{d}
ASPEN	78	16	21	41.8 ± 15.2	---	2698 ± 1125	---	---	5463 ± 1631
GRASSLAND	73	5	7	47.0 ± 22.5	---	1323 ± 1586	---	---	2551 ± 2869^{d}

[a] Number of engorged females that survived and laid eggs.

[b] Statistical tests run on arcsin transformations of these values.

[c] Successful females laid viable eggs, unsuccessful females laid inviable eggs.

[d] Using an F-test for linear combinations of means, these values are significantly different ($p < 0.05$).

* mean $\pm$ 1 SD.

Table 2. Reproductive parameters of engorged female (EF) _Dermacentor albipictus_ at constant 25°C, 1982.

Date Expt. Began	No. of EF	EF Survival No.[a]	EF Survival %	Preoviposition (days)	Incubation (days)	Total Production (eggs/EF)	Percent of Eggs that Hatch (95% CI)[b]	Percent of Larvae that Survive (95% CI)[b]	Reproductive Efficiency Index (eggs/g EF)
3/17	5	3	60	9.0 ± 3.5*	34.0 ± 2.7	5581 ± 2117	100(98, 100)	22(0.2, 76)	8444 ± 1560
3/27	31	20	65	11.0 ± 3.0	36.4 ± 1.9	4043 ± 2436	98(96, 100)	10(2, 21)	7345 ± 1873[c]
4/11	32	15	47	8.3 ± 1.7	37.5 ± 0.8	2902 ± 2250	95(89, 99)	6(2, 13)	6674 ± 1496[c]
4/24	37		6?	7.7 ± 2.9	36.5 ± 9.0	3300 ± 1991	98(96, 99)	35(18, 53)	7198 ± 2568[c]
5/8	25		52	6.4 ± 2.9	37.5 ± 2.0	4481 ± 1489	97(92, 99)	14(2, 34)	8789 ± 1044
5/22	11		91	4.0 ± 1.7[c]	36.2 ± 1.0	4100 ± 1675	98(96, 100)	36(14, 63)	8600 ± 917

[a] Number of engorged females that survived and laid eggs.

[b] Statistical tests run on arcsin transformations of these values.

[c] Using an F-test for linear combinations of means, these values are significantly different ($p < 0.05$).

* mean ± 1 SD.

Table 3. Reproductive parameters of engorged female (EF) _Dermacentor_ _albipictus_ under 19°C and 12:12 photophase, 1983.

Source	Date Expt. Began	No. of EF	EF Survival		Preoviposition Period (days)
			No.[a]	%	
Calves	3/6	14	5	36	19.8 ± 2.7[*]
	3/19	41	27	66	22.4 ± 4.6
	4/2	72	55	76	22.7 ± 4.1
	4/16	38	29	76	20.8 ± 2.8
	4/30	16	15	94	18.9 ± 8.0[b]
	5/14	6	5	83	17.2 ± 5.4[b]
	ALL	187	136	72	21.5 ± 4.7
Reinfested Yearling	3/6	0	0	0	---
	3/19	4	2	50	25.0 ± 1.4
	4/2	31	27	87	22.9 ± 3.3
	4/16	10	9	90	18.6 ± 3.5[b]
	4/30	19	18	95	15.2 ± 3.2[b]
	5/14	19	18	95	15.9 ± 2.2[b]
	ALL	85	76	89	18.9 ± 4.5

[a] Number of engorged females that survived and laid eggs.

[b] Using an F-test for linear combination of means, these values are significantly different ($p < 0.05$).

[*] mean ± 1 SD.

(=date out)(r=-0.603, p<.0001). Length of the preoviposition period decreased slightly with successive drop periods at 19°C (r=-0.239, p=.0050).

At 25°C, percent hatch was high, but larval survival was lower than expected (Table 2). Total production and REI were the only parameters that were positively correlated with EF weight (r=0.908 and 0.393, each p<.0001).

Only two EF in this treatment group laid eggs that failed to hatch.

Reproduction of engorged females after exposure to cold stress

No EF survived the cold stress of freezing at -22°C, and EF survival in the other cold stress treatments was variable (Tables 4, 5, and 6). There was an increasing trend in survival of EF transferred from field conditions to constant 25°C (Table 6) which may be related to the general warming trend in ambient temperatures as spring advanced. Habitat type did not appear to affect either survival or productivity of EF exposed to field conditions (Table 7).

In the three cold stress treatments (10 to 25°C, 0 to 25°C, and field to 25°C), all reproductive parameters except preoviposition period, which generally declined with successive drop periods (r=-0.365, -0.311, -0.709, p=.0008, .0123, <.0001 for 10 to 25°C, 0 to 25°C, and field to 25°C, respectively), were fairly constant between drop periods (Tables 4, 5, and 6). Percent hatch was generally high, but larval survival was variable, particularly for field to 25°C (Table 6). Only total production was significantly correlated with EF weight (r=0.911, 0.847, 0.739, each p<.0001 for 10 to 25°C, 0 to to 25°C, and field to 25°C, respectively). In all three cold stress treatments, all parameters measured were independent of length of cold stress.

Only one and two EF exposed to 10°C and 0°C, respectively, laid eggs that did not hatch.

Reproduction of engorged females under fluctuating temperature and relative humidity

Due to small sample sizes, general trends in the reproductive parameters of EF that laid successful eggs could not be identified for 16 hr -5°C, 8 hr 25°C or 16 hr 0°C, 8 hr 25°C (Tables 8 and 9). Survival of EF in the other three fluctuating treatment groups was

Table 4. Reproductive parameters of engorged female (EF) _Dermacentor albipictus_ transferred from cold stress at 0°C to constant 25°C, 1982.

Date Expt. Began	No. of EF	EF Survival No.[a]	EF Survival %	Preoviposition (days)	Incubation (days)	Total Production (eggs/EF)	Percent of Eggs that Hatch (95% CI)[b]	Percent of Larvae that Survive (95% CI)[b]	Reproductive Efficiency Index (eggs/g EF)
4/4	28	17	61	9.5 ± 6.9*	36.9 ± 4.7	4201 ± 1532	99(98, 100)	98(92, 100)	7754 ± 1535
4/11	28	7	25	9.0 ± 3.1	38.6 ± 2.7	5060 ± 2082	94(73, 100)	100(99, 100)	6732 ± 1916[c]
4/24	27	18	67	7.1 ± 2.4	38.0 ± 2.1	4264 ± 1623	99(98, 100)	88(72, 98)	8352 ± 1403
5/8	12	12	100	5.5 ± 1.2[c]	38.0 ± 1.2	4742 ± 1642	99(96, 100)	70(32, 96)	8607 ± 1584
5/23	11	10	91	6.1 ± 3.8[c]	37.4 ± 4.6	4159 ± 1313	95(73, 100)	68(25, 98)	8539 ± 1208

[a] Number of engorged females that survived and laid eggs.

[b] Statistical tests run on arcsin transformations of these values.

[c] Using an F-test for linear combinations of means, these values are significantly different ($p < 0.05$).

* mean ± 1 SD.

Table 5. Reproductive parameters of engorged female (EF) _Dermacentor albipictus_ transferred from cold stress at 10°C to constant 25°C, 1982.

Date Expt. Began	No. of EF	EF Survival No.[a]	EF Survival %	Preoviposition (days)	Incubation (days)	Total Production (eggs/EF)	Percent of Eggs that Hatch (95% CI)[b]	Percent of Larvae that Survive (95% CI)[b]	Reproductive Efficiency Index (eggs/g EF)
3/27	37	27	73	10.6 ± 7.5*	37.5 ± 2.5	4782 ± 1262	99(99, 100)	97(94, 99)	7953 ± 947
4/11	27	15	56	8.5 ± 2.1	38.5 ± 2.3	5104 ± 1584	93(94, 99)	95(87, 100)	7766 ± 1624
4/24	28	21	75	7.9 ± 2.4[c]	37.9 ± 2.3	4173 ± 1688	99(97, 100)	85(69, 96)	8039 ± 1490
5/8	12	11	92	5.2 ± 1.1[c]	36.8 ± 2.3	4359 ± 1644	99(98, 100)	65(22, 96)	8895 ± 912
5/23	11	7	64	5.6 ± 2.1[c]	35.1 ± 2.7	3828 ± 2057	95(84, 100)	88(45, 100)	7849 ± 1575

[a] Number of engorged females that survived and laid eggs.

[b] Statistical tests run on arcsin transformations of these values.

[c] Using an F-test for linear combinations of means, these values are significantly different ($p < 0.05$).

* mean ± 1 SD.

Table 6. Reproductive paramters of engorged female (EF) _Dermacentor albipictus_ transferred from cold stress under field conditions at Elk Island National Park, Alberta to constant 25°C, 1982.

Date Expt. Began	No. of EF	EF Survival No.[a]	EF Survival %	Preoviposition (days)	Incubation (days)	Total Production (eggs/EF)	Percent of Eggs that Hatch (95% CI)[b]	Percent of Larvae that Survive (95% CI)[b]	Reproductive Efficiency Index (eggs/g EF)
3/27	35	5	14	10.6 ± 3.1*	39.6 ± 2.9	4607 ± 1587	95(88, 99)	4(6, 36)	7027 ± 1494
4/10	45	16	36	8.2 ± 3.0	38.1 ± 2.2	4640 ± 1158	98(96, 100)	11(4, 22)	7923 ± 1923
4/24	52	28	54	5.2 ± 2.6[c]	36.9 ± 5.8	3979 ± 1614	97(95, 99)	14(5, 28)	7358 ± 2088
5/8	15	12	80	2.8 ± 1.6[c]	35.9 ± 1.6	5118 ± 758	99(96, 100)	5(2, 11)	8826 ± 823
5/22	8	8	100	1.9 ± 0.8[c]	36.9 ± 1.6	4666 ± 1012	99(99, 100)	97(94, 99)	9105 ± 61.[c]

[a]Number of engorged females that survived and laid eggs.

[b]Statistical tests run on arcsin transformations of these values.

[c]Using an F-test for linear combinations of means, these values are significantly different (p <0.05).

* mean ± 1 SD.

Table 7. Reproductive parameters of engorged female (EF) *Dermacentor albipictus* transferred from cold stress under field conditions at Elk Island National Park, Alberta to constant 25°C, 1982.

Site	No. of EF	EF Survival No.[a]	EF Survival %	Preoviposition (days)	Incubation (days)	Total Production (eggs/EF)	Percent of Eggs that Hatch (95% CI)[b]	Percent of Larvae that Survive (95% CI)[b]	Reproductive Efficiency Index (eggs/g EF)
BOG	47	19	40	6.1 ± 3.2*	37.7 ± 2.2	4719 ± 1039	98(96, 100)	19(5, 39)	7880 ± 1024
ASPEN	55	24	44	5.8 ± 3.5	37.6 ± 2.0	4493 ± 1667	99(98, 100)	19(5, 35)	7937 ± 1845
GRASSLAND	53	26	49	4.7 ± 3.7	36.5 ± 6.0	4228 ± 1275	97(94, 99)	21(7, 39)	7941 ± 2265

[a] Number of engorged females that survived and laid eggs.

[b] Statistical tests run on arcsin transformations of these values.

* mean ± 1 SD.

Table 8. Reproductive parameters of engorged female (EF) _Dermacentor albipictus_ under fluctuating conditions of -5°C for 16 hours and 25°C for 8 hours, 1982.

Date Expt. Began	No. of EF	EF Survival No.[a]	EF Survival %	Preoviposition (days)	Incubation (days)	Total Production (eggs/EF)	Percent of Eggs that Hatch (95% CI)[b]	Percent of Larvae that Survive (95% CI)[b]	Reproductive Efficiency Index (eggs/g EF)
Successful females[c]									
4/17	45	1	2	10	49	3290	2	0	5708
4/24	26	1	4	8	71	2686	1	0	5276
5/14	12	2	17	15.5 ± 0.7*	138.0 ± 11.3	3112 ± 705	0.2(0.1, 1)	0	6422 ± 908
Unsuccessful females[c]									
4/17	45	17	38	32.4 ± 10.4[d]	---	2898 ± 1548	---	---	4696 ± 1839
4/24	26	16	62	28.1 ± 7.9[d]	---	2745 ± 954	---	---	5500 ± 1380
5/14	12	7	58	16.6 ± 1.8[d]	---	3568 ± 1221	---	---	6106 ± 1845
5/23	11	9	82	13.7 ± 4.6	---	3120 ± 1205	---	---	5698 ± 1079

[a] Number of engorged females that survived and laid eggs.

[b] Statistical tests run on arcsin transformations of these values.

[c] Successful females laid viable eggs, unsuccessful females laid inviable eggs.

[d] Using an F-test for linear combinations of means, these values are significantly different ($p < 0.05$).

* mean ± 1 SD.

Table 9. Reproductive parameters of engorged female (EF) _Dermacentor albipictus_ under fluctuating conditions of 0°C for 16 hours and 25°C for 8 hours, 1982.

Date Expt. Began	No. of EF	EF Survival No.[a]	/ %	Preoviposition (days)	Incubation (days)	Total Production (eggs/EF)	Percent of Eggs that Hatch (95% CI)[b]	Percent of Larvae that Survive (95% CI)[b]	Reproductive Efficiency Index (eggs/g EF)
Successful females[c]									
4/17	38	1	3	24	135	2939	0.1	0	4916
4/24	22	1	5	26	135	3085	0.4	0	7984
5/14	12	1	8	9	130	6174	0.1	0	9633
5/23	12	1	8	12	130	5023	2	0	5339
Unsuccessful females[c]									
4/17	38	20	53	27.9 ± 18.1*	---	3140 ± 1175	---	---	5895 ± 1672
4/24	22	12	55	26.3 ± 8.1	----	3367 ± 1565	---	---	6029 ± 2302
5/14	12	8	67	15.9 ± 4.1	----	2961 ± 958	---	---	6403 ± 933
5/23	12	11	92	13.5 ± 7.5	----	3099 ± 1354	---	---	6719 ± 2274[d]

[a]Number of engorged females that survived and laid eggs.

[b]Statistical tests run on arcsin transformations of these values.

[c]Successful females laid viable eggs, unsuccessful females laid inviable eggs.

[d]Using an F-test for linear combinations of means, these values are significantly different ($p < 0.05$).

* mean $\pm$ 1 SD.

higher (Tables 10, 11, and 12), however, there were only two replicates of 16 hr 25°C, 8 hr 10°C and general trends in reproductive parameters were not tested in this treatment.

The timing of the reproductive cycle under fluctuating conditions was variable. The preoviposition period declined over time under 16 hr 25°C, 8 hr -5°C (r=-0.672, p=.0058) and 16 hr 25°C, 8 hr 0°C (r=-0.771, p<.0001)(Tables 10 and 11). The incubation period for the last two drop periods under 16 hr 25°C, 8 hr -5°C was almost double that for the first two (Table 10), but decreased over time under 16 hr 25°C, 8 hr 0°C (Table 11) (r=-0.460, p=.0071).

Percent hatch was very low in all fluctuating treatments and no larvae survived to the counting date in any treatment group (Tables 8 - 12). Total production and REI were relatively constant over successive drop periods in most of these treatments (Tables 10, 11, 12). Total production and REI were usually positively correlated with EF weight, but REI was negatively correlated with EF weight for 16 hr 25°C, 8 hr -5°C (r=-0.405, p=.0129).

A large proportion of the EF in each of these treatment groups laid eggs which failed to hatch (Tables 8 - 12). The preoviposition period of these EF declined over time as in the other treatments, but the relationship of total production and REI to EF weight and date out was variable between treatment groups.

Table 10. Reproductive parameters of engorged female (EF) <u>Dermacentor apbipictus</u> under fluctuating conditions of -5°C for 8 hours and 25°C for 16 hours, 1982.

Date Expt. Began	No. of EF	EF Survival No.[a]	EF Survival %	Preoviposition (days)	Incubation (days)	Total Production (eggs/EF)	Percent of Eggs that Hatch (95% CI)[b]	Percent of Larvae that Survive (95% CI)[b]	Reproductive Efficiency Index (eggs/g EF)
Successful females [c]									
4/17	41	5	12	12.0 ± 2.1*	50.4 ± 7.2	3395 ± 436	1(0.2, 2)	0	6174 ± 1298
4/24	23	7	30	9.0 ± 2.2	52.6 ± 14.2	3198 ± 846	1(-1, 2)	0	5753 ± 996
5/14	12	3	25	7.3 ± 4.2[d]	98.7 ± 3.5[d]	3653 ± 627	4(-10, 46)	0	7859 ± 367
5/23	12	3	25	6.0 ± 1.7[d]	94.3 ± 7.4[d]	3606 ± 621	1(0, 4)	0	5615 ± 431
Unsuccessful females [c]									
4/17	41	12	29	10.1 ± 4.5	---	3035 ± 1382	---	---	5294 ± 2221
4/24	23	10	44	12.3 ± 3.1	---	2645 ± 882	---	---	6211 ± 1258
5/14	12	9	75	4.8 ± 1.3[d]	---	2963 ± 493	---	---	5635 ± 1075
5/23	12	6	50	4.7 ± 1.5[d]	---	3419 ± 1550	---	---	8229 ± 5428[d]

[a] Number of engorged females that survived and laid eggs.

[b] Statistical tests run on arcsin transformations of these values.

[c] Successful females laid viable eggs, unsuccessful females laid inviable eggs.

[d] Using an F-test for linear combinations of means, these values are significantly different ($p < 0.05$).

* mean ± 1 SD.

Table 11. Reproductive parameters of engorged female (EF) _Dermacentor albipictus_ under fluctuating conditions of $0^{\circ}C$ for 8 hours and $25^{\circ}C$ for 16 hours, 1982.

Date Expt. Began	No. of EF	EF Survival No.[a]	EF Survival %	Preoviposition (days)	Incubation (days)[i]	Total Production (eggs/EF)	Percent of Eggs that Hatch (95% CI)[b]	Percent of Larvae that Survive (95% CI)[b]	Reproductive Efficiency Index (eggs/g EF)
Successful females[c]									
4/17	37	9	24	14.7 ± 4.2*	63.9 ± 14.3	3654 ± 1040	0.6(-0.2, 1)	0	6782 ± 996
4/24	25	8	32	13.0 ± 2.4	63.1 ± 11.1	3436 ± 1051	1(0, 3)	0	6324 ± 1509
5/14	11	7	64	7.6 ± 3.1[d]	52.1 ± 3.4[d]	3453 ± 802	13(3, 27)	0	6507 ± 1748
5/23	11	9	82	5.6 ± .3[d]	52.7 ± 3.9[d]	3324 ± 1314	18(6, 35)	0	7595 ± 1485
Unsuccessful females[c]									
4/17	37	9	24	14.4 ± 5.7	---	3390 ± 1014	---	---	6932 ± 1462
4/24	25	4	16	15.8 ± 5.6	---	3300 ± 1965	---	---	6027 ± 2872
5/14	11	3	27	5.7 ± 2.5[d]	---	2284 ± 977	---	---	4227 ± 1821[d]
5/23	11	2	18	7.5 ± 2.1	---	1625 ± 595[d]	---	---	6057 ± 378

[a]Number of engorged females that survived and laid eggs,

[b]Statistical tests run on arcsin transformations of these values.

[c]Successful females laid viable eggs, unsuccessful females laid inviable eggs.

[d]Using an F-test for linear combinations of means, these values are significantly different ($p < 0.05$).

* mean ± 1 SD.

Table 12. Reproductive parameters of engorged female Dermacentor albipictus under fluctuating conditions of 10°C for 8 hours and 25°C for 16 hours, 1982.

Date Expt. Began	No. of EF	EF Survival No.[a]	%	Preoviposition (days)	Incubation (days)	Total Production (eggs/EF)	Percent of Eggs that Hatch (95% CI)[b]	Percent of Larvae that Survive (95% CI)[b]	Reproductive Efficiency Index (eggs/g EF)
Successful females[c]									
5/22	64	8	13	33.0 ± 17.2*	109.3 ± 10.6	2117 ± 1141	1(0.2, 2)	0	4350 ± 1797
5/23	11	4	36	28.5 ± 10.2	76.6 ± 51.3	2902 ± 1048	1(-0.1, 5)	0	5243 ± 1618
Unsuccessful females[c]									
5/20	64	26	35	36.3 ± 17.3	---	1433 ± 964	---	---	2882 ± 1855
5/23	11	6	6	36.5 ± 8.5	---	692 ± 322[d]	---	---	2160 ± 822[d]

[a] Number of engorged females that survived and laid eggs.

[b] Statistical tests run on arcsin transformations of these values.

[c] Successful females laid viable eggs, unsuccessful females laid inviable eggs.

[d] Using an F-test for linear combinations of means, these values are significantly different ($p < 0.05$).

* mean ± 1 SD.

APPENDIX 9.   Calculations for use in the flow rate model of Dermacentor

albipictus in Elk Island National Park, Alberta.

Calculations of parasite flow rates were organized in a 4 x 3 matrix with the four ungulate host species assigned to rows and the three habitat types assigned to columns. Host density was obtained from population estimates provided by Blyth (unpub). Habitat usage and habitat proportions are from Cairns (1976).

For ease of calcuation, a ranking system was used for the abundance of ticks per host individual. An average of 36,969 ticks per moose, 11,638 ticks per wapiti, 2,700 ticks per deer, and 36 ticks per bison were found on hides collected from 1977 to 1983 in EINP (Samuel, unpub). Moose were assigned a rank of 1.0, while wapiti, deer, and bison were given ranks of 0.3, 0.07, and 0.001, respectively.

All cell products in a row were summed, as were all cell products of a column. Each row sum was divided by the grand sum to calculate the relative flow rate of EF *Dermacentor albipcitus* from each host species to the tick population (A). To determine the flow rate from the tick population into each habitat type, each column sum was divided by the grand sum.

To obtain flow rates of larvae to each host species and from each habitat type, additional cells on EF productivity were added to the calculations (B). Habitat specific mortality rates and reproductive parameters of *D a'bipictus* are from the preceding chapters. Row sums were divided by the grand sum to obtain flow rates of larvae from the tick population to each host species while column sums were divided by the grand sum to obtain flow rates of larvae from the three habitat types to the tick population.

Similar calculations were performed to obtain fow rates of EF and larvae between each host species and each habitat type while assuming a low moose population and all other host species at carrying capacity (C and D).

Calculations of flow rates of <u>Dermacentor albipictus</u> from host species to the tick population and from the tick population to habitat type assuming all host populations at carrying capacity.

Host Species	Habitat Type			Row Sum
	Bog	Aspen	Grassland	
Moose				
Density (#/ha)	0.020	0.020	0.020	
<u>D.a.</u> Abundance	1.0	1.0	1.0	
Habitat Usage	6.0	85.0	9.0	
Habitat Prop.	7.0	79.0	14.0	
Prop. EF Drop	1.5	1.5	1.5	
PRODUCT	1.26	201.45	3.78	206.49
Wapiti				
Density (#/ha)	0.025	0.025	0.025	
<u>D.a.</u> Abundance	0.3	0.3	0.3	
Habitat Usage	3.0	78.0	19.0	
Habitat Prop.	7.0	79.0	14.0	
Prop. EF Drop	1.5	1.5	1.5	
PRODUCT	0.33	69.32	2.99	72.64
Deer				
Density (#/ha)	0.015	0.015	0.015	
<u>D.a.</u> Abundance	0.07	0.07	0.07	
Habitat Usage	4.0	86.0	10.0	
Habitat Prop.	7.0	79.0	14.0	
Prop. EF Drop	1.5	1.5	1.5	
PRODUCT	0.04	10.70	0.22	10.96
Bison				
Density (#/ha)	0.031	0.031	0.031	
<u>D.a.</u> Abundance	0.001	0.001	0.001	
Habitat Usage	5.0	62.0	33.0	
Habitat Prop.	7.0	79.0	14.0	
Prop. EF Drop	1.5	1.5	1.5	
	0.002	0.23	0.02	0.25
COLUMN SUM	1.63	281.70	7.01	
GRAND SUM	290.34			

B

Calculation of flow rates of <u>Dermacentor albipictus</u> from the tick population to host species and from habitat type to the tick population assuming all host populations at carrying capacity.

Host Species	Habitat Type			Row Sum
	Bog	ASpen	Grassland	
Moose				
Previous Product A	1.26	201.45	3.78	
%EF Survival	0.34	0.13	0.37	
#eggs/EF	3227	3013	3152	
%egg Hatch	0.51	0.23	0.59	
PRODUCT	705.05	18148.37	1733.97	20587.39
Wapiti				
Previous Product A	0.33	69.32	2.99	
%EF Survival	0.34	0.13	0.37	
#eggs/EF	3227	3013	3152	
%egg Hatch	0.51	0.23	0.59	
PRODUCT	132.20	6245.17	2059.08	8436.45
Deer				
Previous Product A	0.04	10.70	0.22	
%EF Survival	0.34	0.13	0.37	
#eggs/EF	3227	3013	3152	
%egg Hatch	0.51	0.23	0.59	
PRODUCT	24.68	964.00	151.72	1140.40
Bison				
Previous Product A	0.002	0.23	0.02	
%EF Survival	0.34	0.13	0.37	
#eggs/EF	3227	3013	3152	
%egg Hatch	0.51	0.23	0.59	
PRODUCT	0.91	20.52	14.78	36.21
COLUMN SUM	862.84	25378.06	3959.55	
GRAND SUM	30200.45			

Calculation of flow rates of <u>Dermacentor</u> <u>albipictus</u> from host species to the tick population and from the tick population to habitat type assuming <u>low moose populations and all other host populations at carrying capacity.</u>

Host Species	Habitat Type			Row Sum
	Bog	Aspen	Grassland	
<u>Moose</u>				
Density (#/ha)	0.005	0.005	0.005	
<u>D.a</u>. Abundance	1.0	1.0	1.0	
Habitat Usage	6.0	85.0	9.0	
Habitat Prop.	7.0	79.0	14.0	
Prop. EF Drop	1.5	1.5	1.5	
PRODUCT	0.32	130.61	4.18	51.63
<u>Wapiti</u>				
Density (#/ha)	0.025	0.025	0.025	
<u>D.a</u>. Abundance	0.3	0.3	0.3	
Habitat Usage	3.0	78.0	19.0	
Habitat Prop.	7.0	79.0	14.0	
Prop. EF Drop	1.5	1.5	1.5	
PRODUCT	0.33	69.32	2.99	72.64
<u>Deer</u>				
Density (#/ha)	0.015	0.015	0.015	
<u>D.a</u>. Abundance	0.07	0.07	0.07	
Habitat Usage	4.0	86.0	10.0	
Habitat Prop.	7.0	79.0	14.0	
Prop. EF Drop	1.5	1.5	1.5	
PRODUCT	0.04	10.70	0.22	10.96
<u>Bison</u>				
Density (#/ha)	0.031	0.031	0.031	
<u>D.a</u>. Abundance	0.001	0.001	0.001	
Habitat Usage	5.0	62.0	33.0	
Habitat Prop.	7.0	79.0	14.0	
Prop. EF Drop	1.5	1.5	1.5	
PRODUCT	0.002	0.23	0.02	0.25
COLUMN SUM	0.69	130.61	4.18	
GRAND SUM.	135.48			

D

Calculation of flow rates of Dermacantor albipictus from the tick population to host species and from habitat type to the tick population assuming a low moose population and all other host populations at carrying capacity.

Host Species	Habitat Type			Row Sum
	Bog	Aspen	Grassland	
Moose				
Previous Product C	0.32	130.61	4.18	
%EF Survival	0.34	0.13	0.37	
#eggs/EF	3227	3013	3152	
%egg Hatch	0.51	0.23	0.59	
PRODUCT	176.26	4537.09	650.23	5363.58
Wapiti				
Previous Product C	0.33	69.32	2.99	
%EF Survival	0.34	0.13	0.37	
#eggs/EF	3227	3013	3152	
%egg Hatch	0.51	0.23	0.59	
PRODUCT	132.20	6245.17	2059.08	8436.45
Deer				
Previous Product C	0.04	10.70	0.22	
%EF Survival	0.34	0.13	0.37	
#eggs/EF	3227	3013	3152	
%egg Hatch	0.51	0.23	0.59	
PRODUCT	24.68	964.00	151.72	1140.40
Bison				
Previous Product C	0.002	0.23	0.02	
%EF Survival	0.34	0.13	0.37	
#eggs/EF	3227	3013	3152	
%egg Hatch	0.51	0.23	0.59	
PRODUCT	0.91	20.52	14.78	36.21
COLUMN SUM	334.05	11766.78	2875.81	
GRAND SUM	14976.64			

APPENDIX 10. Proportion of the numbers of engorged female Dermacentor

albipictus that drop off moose on specific dates.

| SNOWMELT DATE | ENGORGED FEMALES DROPPING | | SNOWMELT DATE | ENGORGED FEMALES DROPPING | |
	BEFORE SNOWMELT (D^1)	AFTER SNOWMELT (D^2)		BEFORE SNOWMELT (D^1)	AFTER SNOWMELT (D^2)
Feb. 27	0.016	0.984	Apr. 1	.531	.469
28	.031	.969	2	.547	.453
Mar. 1	.047	.953	3	.563	.438
2	.063	.938	4	.578	.422
3	.078	.922	5	.594	.406
4	.094	.906	6	.609	.391
5	.109	.891	7	.625	.375
6	.125	.875	8	.641	.359
7	.141	.859	9	.656	.344
8	.156	.844	10	.672	.328
9	.172	.828	11	.688	.313
10	.188	.813	12	.703	.297
11	.203	.797	13	.719	.281
12	.219	.781	14	.734	.266
13	.234	.766	15	.750	.250
14	.250	.750	16	.766	.234
15	.266	.734	17	.781	.219
16	.281	.719	18	.797	.203
17	.297	.703	19	.812	.188
18	.313	.688	20	.828	.172
19	.328	.672	21	.844	.156
20	.344	.656	22	.859	.141
21	.359	.641	23	.875	.125
22	.375	.625	24	.891	.109
23	.391	.609	25	.906	.094
24	.406	.594	26	.922	.078
25	.422	.578	27	.938	.063
26	.438	.563	28	.953	.047
27	.453	.547	29	.969	.031
28	.469	.531	30	.984	.016
29	.484	.516	May 1	1.000	0.000
30	.500	.500			
31	.516	.484			

APPENDIX 11. An evaluation of burning for control of winter ticks

in central Alberta. (To be submitted to the Journal

of Wildlife Disease).

. INTRODUCTION

The winter tick, *Dermacentor albipictus*, is a one-host tick found on moose and other large ungulates throughout much of North America. Infestations of moose are seasonal; moose acquire larvae in autumn with peak exposure in early October, nymphs overwinter on the host, and adults emerge and feed in spring (Drew, unpub). Females engorge and drop from the host from February to May. Under field conditions in central Alberta, egg laying begins in early June and hatching occurs in late August and early September (Drew, unpub).

Levels of infestation on moose in central Alberta often exceed 50,000 ticks per moose (Samuel and Barker, 1979; Glines, 1983; Samuel, unpub). The high tick loads cause infested moose to groom and remove much of their winter hair two to three months prematurely. In an effort to control infestations of winter ticks on moose, the effects of a prescribed burn on survival and productivity of engorged female *D. albipictus* was investigated.

MATERIALS AND METHODS

The prescribed burn was conducted on 12 May, 1982 in Elk Island National Park, about 40 km east of Edmonton, Alberta. The purpose of the burn was to examine the effectiveness of spring burning for killing old growth aspen (*Populus tremuloides*), initiating browse regeneration, and opening areas to allow expansion of existing . grasslands.

Engorged female *D. albipictus* were collected from March to April, 1982 from bedding sites of free-ranging moose in Elk Island National Park and from captive moose housed at the University of Alberta Biomedical Animal Center, Ellerslie, Alberta. A total of 264 engorged females was collected and stored at 10°C until 3 May, 1982. Thirty-three females were released in each of eight sites in the designated burn site in Elk Island National Park on 3 May, 1982 (Table 1). Release sites were marked with surveyor's flagging tape and metal poles.

Immediately after the burn, all release sites were checked for degree of duff burned, presence or absence of engorged females, and the status of a few of the females

Table 1. Survival of engorged female (EF) and recovery of larval
Dermacentor albipictus after a prescribed burn in Elk Island
National Park, Alberta in spring, 1982.

Site # and Habitat	# EF Released	Estimated # EF that Survived[a]	Survival (%)	Duff Burned (%)	# Larvae Flagged[b]
1 - dense canopy aspen moderate shrub understory	33	0	0	75	0
2 - dense canopy aspen moderate shrub understory	33	6	18.2	25	18,888
3 - dense canopy aspen moderate shrub understory	33	0	0	75	0
4 - willow overstory grassy understory	33	0	0	75	64
5 - open canopy aspen grassy understory	33	0	0	50	9
6 - open canopy aspen grassy understory	33	1	3.0	50	1,913
7 - grassland	33	1	3.0	75	1,114
8 - grassland	33	0	0	100	2
TOTAL	265	8	3.0		21,990

[a]Based on an average of 3000 larvae produced per EF (Drew, 1984).

[b]Less than 100 larvae recovered per site was regarded as an indication of contamination.

found. Each site was flagged for larvae using a 0.5 sq m white flannel cloth on a wooden pole four times from 4 October to 1 November, 1982. Larvae on the flags were counted using a small vacuum apparatus in the laboratory.

RESULTS AND DISCUSSION

Over 95% of the engorged females died in areas that were burned (Table 1). Higher survival rates of engorged females occurred in the dense canopy aspen (Table 1, Site 2), and was attributed to the incomplete burning (25%) of the duff and litter. Survival of engorged females is also affected by weather conditions. Survival of engorged females after snowmelt averaged 60% to the onset of oviposition in June and 28% at the time of egg hatching in September in three control sites (bog, aspen forest, and grassland) in Elk Island National Park the same spring (Drew, unpub). If engorged females in the burn site had similar survival rates prior to burning, burning increased mortality by about 25%.

Recovery of larvae by flagging in autumn indicated that a few of the engorged females survived the burn. Variable, but low numbers of larvae were recovered at six of the eight release sites (Table 1), suggesting that the burn was effective in reducing, but not in eliminating, the numbers of larvae available to moose in autumn.

Fire is effective in reducing populations of *Amblyomma americanum* (Jacobson and Hurst, 1979; Oldham et al. 1981) and *Ixodes scapularis* (Roberts, 1955). However, these reports concern prescribed burning in grassland habitats. The vegetation in open grassy areas tends to be almost totally burned (Wright, 1974), therefore, burning in these areas would be most effective for controlling ticks.

Burning of forested habitat types usually removes the leaf litter but does not completely burn the soil duff layer. Variability in vegetation density, amount of fuel, and moisture content of the fuel make control and preditions of the degree of burning difficult (Drawe, per comm). Hoch et al. (1972) found that controlled burning in oak-hickory woodlots was not effective in reducing populations of *A. americanum* due to incomplete burning of the duff.

Burning may also be unreliable for winter tick control in central Alberta due to these factors. Success will probably be determined by the habitat type being burned,

weather conditions prior to the burn, and the fuel load in the burn site. A slow, hot fire must be maintained by a sufficient quantity of fuel to ensure adequate burning of the duff and litter layer where the engorged females are. The period between snowmelt and leaf out in spring is probably the best time of the year for burning to control the numbers of engorged females that survive and lay eggs and, thus, for reducing the numbers of larvae available for transmission in autumn.

A fall burn to reduce the numbers of larvae available would probably be very effective since most larvae are at or near the tips of the vegetation waiting for a host (Drew, unpub). These larvae do not descend to the duff once they have ascended vegetation, a behavior that increases their suspectibility to fire. A hot, fast fire would possibly kill a large proportion of the larvae, but would have to be done between early September and early October before the period of peak transmission (Drew, unpub). However, a fall burn would also decrease the amount of forage available for ungulates during the winter following the burn. An annual, rotating schedule for burning small areas may alleviate this problem and provide an effective means for reducing the numbers of ticks per moose in areas of high infestation levels.

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