

Climbing Simulated Vegetation to Heights of Ungulate Hosts by Larvae of *Dermacentor albipictus* (Acari: Ixodidae)

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ABSTRACT Larvae of winter ticks, *Dermacentor albipictus* (Packard), ascend vegetation in autumn and form clumps that attach to passing ungulate hosts. We tested the hypothesis that vegetation height determines the height of clumps. During the vegetation-to-ungulate transmission period (early September to mid-November), larvae were released at the base of simulated vegetation (nylon rods 245 cm tall) in outdoor and laboratory trials and in the absence of host cues. Rod height exceeded the height of the tallest ungulate host, which is the moose, *Alces alces* (L.). Most larvae stopped climbing and formed clumps 50–190 cm above ground, which coincided with torso heights of moose; elk, *Cervus elaphus* L.; and deer, *Odocoileus* spp. *Rafinesque*. More clumps formed in outdoor trials than in laboratory trials and clump heights tended to increase over the course of the experiment, but clump number, size, and height did not correlate with weather conditions. Winter tick larvae appear to determine their height above ground in the absence of external cues, but this mechanism may be modified by external conditions.

KEY WORDS *Dermacentor albipictus*, adaptations, behavior, host-finding, larvae, transmission

THE WINTER TICK, *Dermacentor albipictus* (Packard), is a 1-host tick found commonly on North American members of the Cervidae (Anderson and Lankester 1974), especially moose, *Alces alces*; elk, *Cervus elaphus*; and deer, *Odocoileus* spp. (Welch et al. 1991). Moose are the most seriously affected host (Welch et al. 1991); tick infestations cause anemia and other physiological problems, depletion of fat stores, and grooming-induced breakage and loss of hair (Samuel and Barker 1979, McLaughlin and Addison 1986, Glines and Samuel 1989, Samuel 1991). Individual moose often have >50,000 ticks (Samuel and Welch 1991), and tick-associated die-offs of moose are frequent (Samuel and Barker 1979, Addison and Smith 1981, Blyth 1995).

In Alberta, larvae of *D. albipictus* ascend vegetation, form clumps, and remain on vegetation from early September to mid-November with highest numbers in October (Drew and Samuel 1985, Samuel and Welch 1991). In the field, number of larvae in a clump range from 10 to ≈1,000 (Drew and Samuel 1985). Once ungulate hosts become infested, ticks develop into nymphs and adults on the same individual host during winter and spring. Larvae that do not infest hosts in the autumn die when winter comes (Samuel and Welch 1991). Engorged adult females drop from hosts in April (Drew and Samuel 1989). Lees (1948), Lees and Milne (1951), Wilkinson (1953), Camin and Drenner (1978), and Loye and Lane (1988) hypothesized that

Ixodes ricinus L., *Boophilus microplus* (Canestrini), *Hemaphysalis leporispalustris* (Packard), and *Ixodes pacificus* Cooley and Kohls, respectively, position themselves on vegetation at mean heights, or within height ranges, corresponding to the body heights of primary hosts.

Drew and Samuel (1985) and Aalangdong (1994) suggested that vegetation height determined where clumps of winter tick larvae formed on vegetation in central Alberta. Objectives of the current study were to determine whether or not: (1) larvae of *D. albipictus* would form clumps on simulated vegetation at the heights of their preferred ungulate hosts; (2) climbing activity of larvae would change over the course of the natural transmission period in autumn; and (3) weather had any effect on climbing behavior and clump formation.

Materials and Methods

Ticks. Engorged female *D. albipictus* were collected from 3 moose carcasses in central Alberta (2 adults were killed on highways and 1 calf died of natural causes) in mid-April to mid-May 1997. Ticks were maintained over water in incubators at 20°C and ≈95% RH next to a window to expose them to natural light and photoperiod. Approximately 150 ticks oviposited between 13 May and 26 June and eggs began to hatch 4 July. Larvae from mixed egg masses were kept in mesh-covered glass vials, 700–900 per vial, over water in incubators until used in climbing experiments.

Design. Each climbing apparatus (Fig. 1) was a rod suspended from the ceiling indoors and from a

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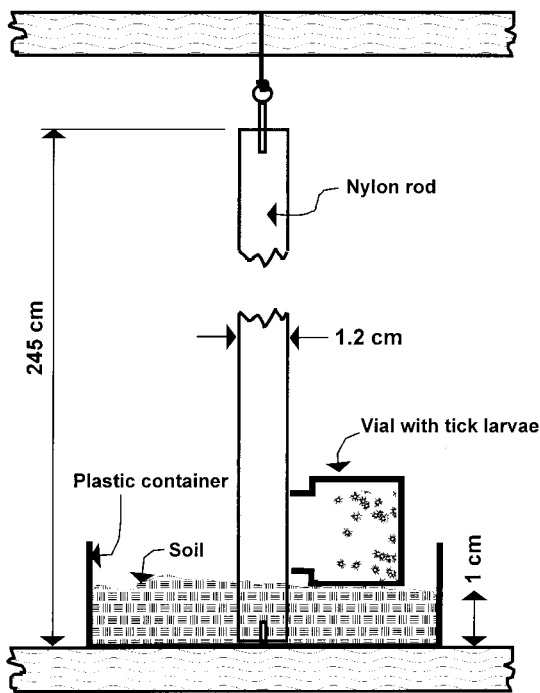


Fig. 1. Construction details of apparatus for tick climbing experiments.

wooden frame outdoors, with moistened soil at its base. We used Polypenco² annealed nylon rods that had extremely smooth, impermeable surfaces, because tick larvae form clumps on surfaces with minor imperfections (Camin and Drenner 1978; W.M.S., unpublished data) and permeable surfaces could result in uptake of human odors that might affect tick behavior. Apparatuses were grouped in sets of 4, with 45 cm between rods and double-sided tape surrounding the base of each apparatus. Rod heights (245 cm) exceeded the average shoulder height of adult male moose (190 cm, Stelfox and Stelfox 1993), the largest preferred host.

Each trial was a set of identical experiments done simultaneously using 1 set of 4 rods in each of 3 locations (12 rods total). Locations were outdoors on a west-facing roof-top patio of the University of Alberta's Biological Sciences Building (hereinafter called "outdoors"); a laboratory at $\approx 20^{\circ}\text{C}$ with an east-facing window ("indoors with natural light"); and a laboratory at $\approx 20^{\circ}\text{C}$ with no windows but with constant overhead fluorescent lighting ("indoors with constant light"). Thirteen trials, each 48 h long, were done at each location on a nearly biweekly schedule, as follows: trial 1 (10–12 September), 2 (15–17 September), 3 (22–24 September), 4 (24–26 September), 5 (29 September–1 October), 6 (1–3 October), 7 (6–8 October), 8 (14–16 October), 9 (20–22 October), 10 (22–24 October), 11 (27–29 October), 12 (29–31 October), and 13 (3–5 November).

Before each trial, rods were cleaned with 95% ethanol and soil was replaced to remove human odors and

ticks. Twelve vials of larvae were removed from the incubator before each trial, and 1 vial chosen at random was opened and placed at the base of each rod. The vial was laid on its side with the top and bottom of the mouth in contact with the rod (Fig. 1). Each batch of larvae was used in only 1 trial.

Trials were begun between 0800 and 1000 hours. Observations were recorded as follows: 24 h and 48 h after the start of each trial: the number of clumps (aggregations of 4 or more larvae) on each rod; clump height (distance from soil surface to center of clump); number of ticks per clump (exact count until numbers approached 200, above which numbers were estimated); and at the outdoors location only, the orientation of clumps (north, east, west, south). Occasionally, ticks were seen on the apparatus above the rods. These were included in the count of clumps, but not ticks per clump. Clumped larvae sometimes scattered as the observer approached, and in these cases no data were recorded from any of the rods in that location at that time.

Meteorological data were obtained from the University of Alberta Weather Station located on the roof of an adjacent building. Data included minimum and maximum temperature and relative humidity, solar radiation, average wind speed and precipitation for the day each trial started and 24 h later when observations were first made.

Data Analysis. Statistical testing was done following the recommendations of Zar (1996), and was implemented using SYSTAT 8.0 for Windows statistical software, or routines written using the Quattro Pro 7.0 spreadsheet program. Preliminary analysis (Wilcoxon signed-rank test) indicated that there was no significant change in distribution between the 24- and 48-h observations for clump height ($P = 0.056$), number of clumps per rod ($P = 0.445$), and ticks per clump ($P = 0.085$), so only the 24-h results are presented herein.

Data sets in some trials were incomplete; trial 1 in all locations (most larvae remained in the vials); trials 7 and 12 indoors with natural light and trials 4–7 and 12 indoors with constant light (scattering of clumps as observer approached); and trial 10 outdoors (larvae remained in vials apparently because of a snowfall). Trials were pooled into 4 groups because of the incomplete data sets: period 1 (trials 2–4), period 2 (trials 5–7), period 3 (trials 8–10), and period 4 (trials 11–13).

Clump heights were partitioned into 3 biologically relevant zones based on reported heights (Renecker and Hudson 1993) of ungulate hosts, as follows: zone 1, < 50 cm, was considered too low for transmission to ungulate hosts because it is below the chest height of juvenile white-tailed deer, *Odocoileus virginianus* (Zimmermann); zone 2, from 50 to 190 cm, was considered to be suitable for transmission because it spans the chest height of juvenile white-tailed deer to the shoulder height of adult moose; zone 3, > 190 cm, was considered too high for transmission because it is above the shoulder height of adult moose. Zones 1, 2, and 3 contained 20.4, 57.1, and 22.5%, respectively, of

the surface area of the test rods. The null hypothesis that the number of clumps of ticks in zones 1, 2, and 3 was in the same ratio as the surface area of each zone, was tested with a chi-square goodness-of-fit test to a 0.204:0.571:0.225 ratio. The consistency of distribution among zones for all period \times location combinations was tested using a chi-square test of heterogeneity.

Numbers of clumps, clump heights, and numbers of ticks per clump in most period \times location combinations were non-normally distributed (Kolmogorov-Smirnov test, $P > 0.05$, and visual examination of cumulative distributions against a normal probability scale) and standard data transformations were effective in only some combinations. Therefore, nonparametric statistics were used throughout. Differences among rods in the different locations were tested using Kruskal-Wallis or Mann-Whitney tests. If the overall test was significant, nonparametric Tukey-type multiple comparisons were done, using the Nemenyi test. Trends over time were tested using Spearman rank correlations. The mean angle and mean angular deviation of clumps outdoors was calculated, with magnetic north considered 0° , and east as 90° . Comparison of clump orientation among periods was by chi-square test of independence, after pooling the data from south and west orientations to minimize cells with sparse data.

Results

Height of Clumps. Larvae of *D. albipictus* climbed and formed clumps within 24 h. The median height of clumps was 112 cm ($n = 434$; mean = 125; SD = 58; range, 24.1–245 cm).

There was significant heterogeneity among periods and locations in the distribution of ticks among zones ($P < 0.001$), so data were not pooled. Compared with the null hypothesis of a 0.204:0.571:0.225 ratio, ticks formed clumps significantly more often ($P < 0.05$) in zone 2, and less often in zones 1 and 3 in 8 of 11 period \times location combinations, and there was a marginally significant excess ($P < 0.10$) in zone 2 in 2 other combinations (Fig. 2). Zone 2 comprised 57.1% of the test rod surface area but harbored 63–100% of the tick clumps in the 11 combinations.

The distribution of clump heights (Fig. 3) did not differ among the outdoor and 2 indoor locations for any period (period 1, $P = 0.252$; period 2, $P = 0.950$; period 3, $P = 0.080$; period 4, $P = 0.712$). Clump heights were correlated with period at the outdoors ($r = 0.19$, $n = 289$, $P < 0.001$) and indoors with natural light ($r = 0.38$, $n = 44$, $P < 0.01$) locations, but not indoors with constant light ($r = -0.01$, $n = 67$, $P > 0.50$).

Number of Clumps per Rod. Ticks formed a median of 3 clumps per rod ($n = 106$ rods, mean = 4.1, SD = 4.5, range 0–22). Number of clumps per rod (Fig. 3) differed significantly among the 3 locations in period 1 ($P = 0.009$; Nemenyi test: outdoors $>$ indoors with natural light, $P < 0.05$), and period 3 ($P = 0.05$; Nemenyi test: no pairs differed significantly), but not period 4 ($P = 0.103$). In period 2, with data from only 2

locations, more clumps formed outdoors than indoors with natural light ($P < 0.001$). The number of clumps was not correlated with period at the outdoors ($r = 0.18$, $n = 44$, $P > 0.20$), indoors with natural light ($r = 0.26$, $n = 36$, $P > 0.10$), or indoors with constant light ($r = 0.31$, $n = 26$, $P > 0.10$) locations.

Number of Ticks per Clump. There was a median of 19 ticks per clump ($n = 400$ clumps, mean = 30, SD = 31, range 4–210), with a highly skewed distribution (Fig. 4). Some clumps that formed at the tops of the rods could not be counted but were estimated to contain >300 ticks. Based on the shape of the distribution (Fig. 4), large clumps were clearly an exception and 85% contained fewer than 50 larvae.

The number of ticks per clump (Fig. 3) did not differ significantly among locations (Kruskal-Wallis test) during period 1 ($P = 0.157$), period 2 ($P = 0.422$), or period 3 ($P = 0.180$). There was a difference among locations during period 4 ($P = 0.008$; Nemenyi test: indoors with constant light $>$ outdoors, $P < 0.01$). The number of ticks per clump was not correlated with period outdoors ($r = -0.04$, $n = 289$, $P > 0.50$) or indoors with constant light ($r = -0.05$, $n = 67$, $P > 0.50$), but increased significantly during the course of the study indoors with natural light ($r = 0.40$, $n = 44$, $P < 0.01$).

Ticks per clump was negatively correlated with clump height during period 2 ($r = -0.21$, $n = 140$, $P < 0.05$) and positively correlated with height during period 4 ($r = 0.28$, $n = 53$, $P < 0.05$). There was no correlation ($P > 0.10$) in the remaining 9 period \times location combinations. Zone 2 comprised 57.1% of the rod surface but harbored 68–100% of the individual ticks in the 11 combinations.

General Observations. After 16 September, ticks disturbed by the observer assumed a questing posture at the outdoors location, whereas ticks indoors tended to scatter upwards. Outdoors, there were many slow-moving, nonclumped ticks on all rods after 14 October.

The orientation of clumps outdoors varied among periods ($P < 0.001$). Clumps outdoors were generally oriented east for periods 1, 3, and 4 (mean angle \pm mean angular deviation were 88 ± 30 , 77 ± 33 and 83 ± 26 degrees, respectively) and east-northeast during period 2 (41 ± 52 degrees).

Temperature, solar radiation, and wind speed were negatively correlated with trial ($r = -0.659$, $n = 13$, $P < 0.05$; $r = -0.676$, $n = 13$, $P < 0.05$; $r = -0.683$, $n = 13$, $P < 0.05$, respectively), but the decline was not monotonic (Fig. 5). Daily maximum and minimum relative humidities averaged 93 and 62%, but fell as low as 35% during trial 3. Rain fell during trials 2, 4, 6, 9, and 10, and there was snowfall during trial 10. The median numbers of clumps, clump heights, and ticks per clump for each outdoors trial were not correlated ($P > 0.10$) with any weather variables recorded at the start of that trial, with 1 exception. Median clump height was positively correlated with wind speed ($r = 0.633$, $n = 11$, $P < 0.05$).

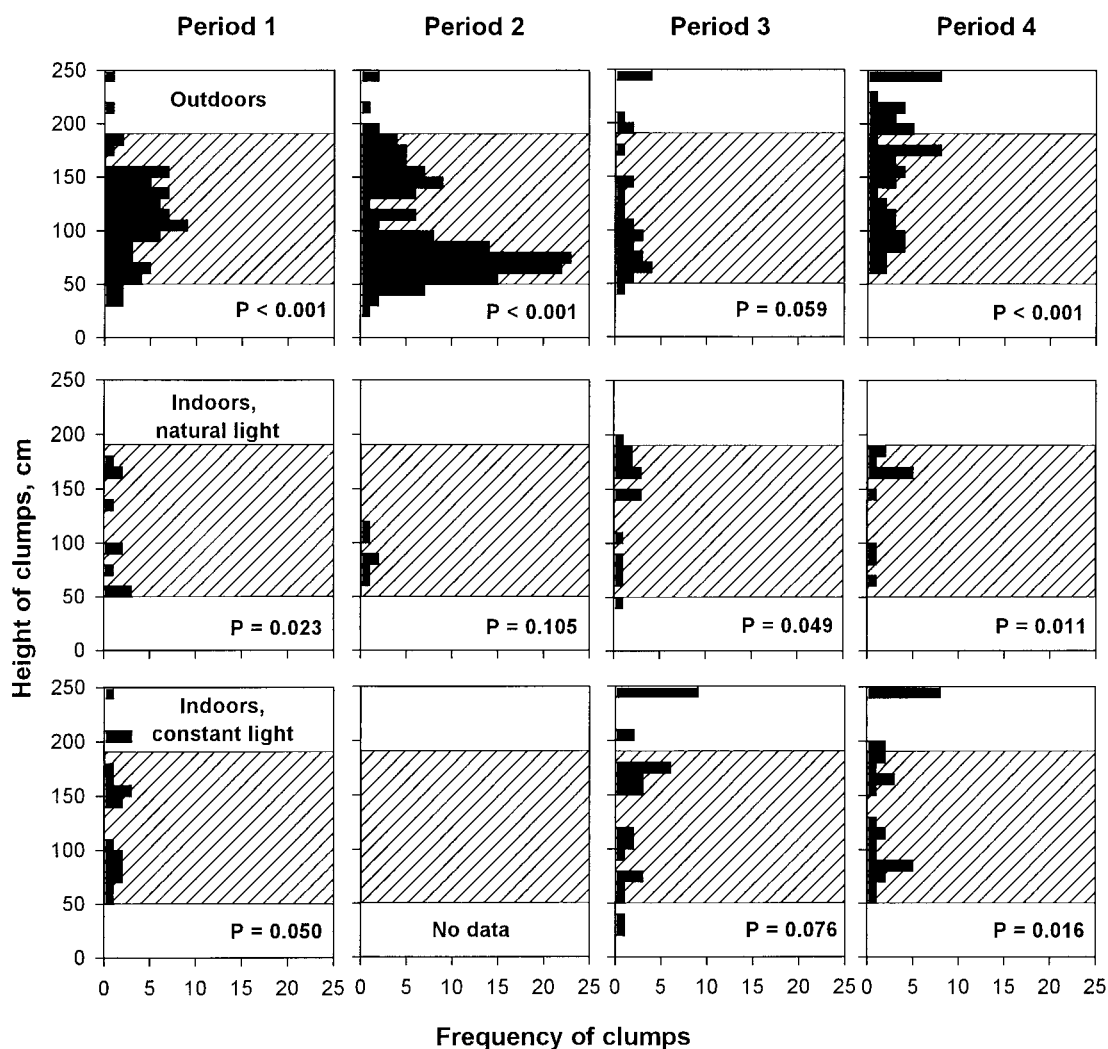


Fig. 2. Frequency distribution of heights of clumps of tick larvae 24 h after introduction to the test apparatus, separated by time period and location. The hatched area represents the range of heights likely to facilitate transmission. Probability values are from chi-square goodness-of-fit test for the number of clumps to a ratio of 0.204 (<50 cm), 0.571 (50–190 cm), 0.225 (>190 cm).

Discussion

Larvae of *D. albipictus* ascend vegetation in autumn and form clumps that attach to passing ungulate hosts, moose, elk, and deer. Once formed, clumps remain intact in the same position on vegetation except when they transfer to a host, are blown off, get covered with snow, or die (Drew and Samuel 1985, Samuel and Welch 1991). Drew and Samuel (1985) found that the mean height (≈ 1 m) of clumps on vegetation in Elk Island National Park, Alberta, was close to the mean height of available vegetation. They concluded that vegetation height constrained height of tick clumps on vegetation. Height was not a constraint in the current study, because ticks could climb well above the heights of their preferred hosts, moose, elk, and deer. Most larvae ceased climbing and formed in clumps

50–190 cm above ground level, which coincides with torso heights of deer, elk, and moose. This suggests that larvae are able to determine their height above ground in the absence of cues from climbing surfaces or hosts.

Results are in general agreement with those of previous studies that used arena systems with glass or wooden rods; ticks tend to select and climb rods that approximate the height of their host. Larvae of the rabbit tick, *H. leporispalustris*, choose and climb to the tips of rods 7–19 cm high, a height approximating that of rabbits (Camin and Drenner 1978), in preference to rods 1–4 or 22–28 cm high. Adult *I. pacificus* appear to have a height preference of ≈ 50 cm, which “facilitates contact with the venter and legs of deer and other medium-sized to large mammals, including lagoon-

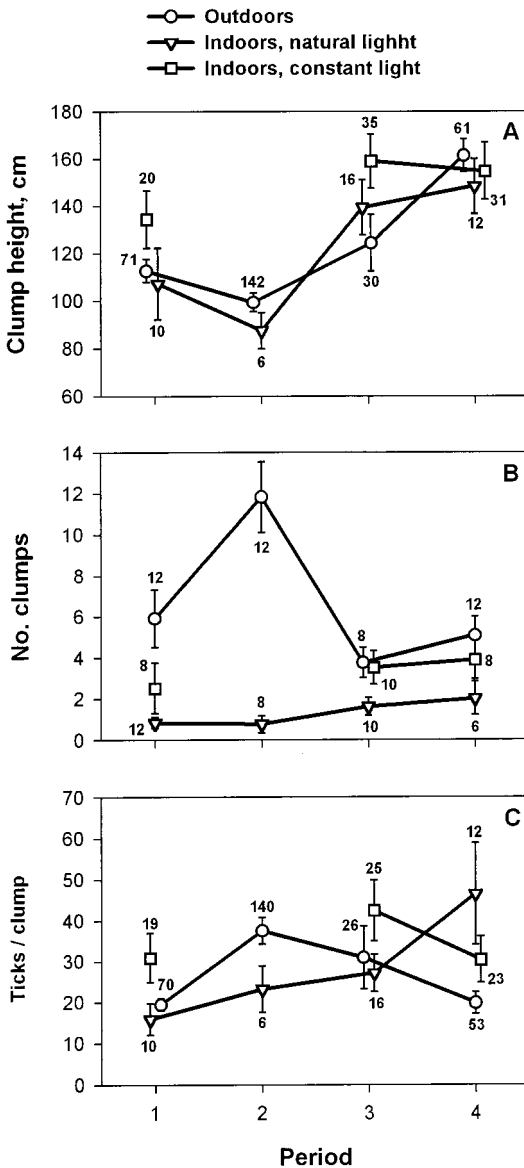


Fig. 3. Characteristics of clumps of tick larvae recorded during various time periods 24 h after introduction to the test apparatus: (A) Height of clumps. (B) Number of clumps on each rod. (C) Number of ticks per clump. Values represent mean \pm SE. Sample size is indicated next to each bar.

morphs and carnivores" (Loye and Lane 1988). The observation that shorter rods (25 and 50 cm high) had many ticks at the tips, but rods 75 cm high had fewer ticks that ascended only partially, prompted Loye and Lane (1988) to suggest that adult *I. pacificus* reject tall substrates as potential questing sites.

In the current study, climbing activity was not influenced by pits or bumps, as might occur on vegetation, because smooth nylon rods were used. In addition, rods were devoid of host cues such as odor, heat or CO₂, which are believed to stimulate host-seeking

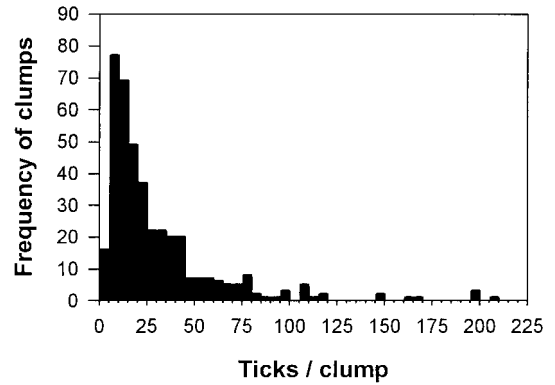


Fig. 4. Frequency distribution of the number of tick larvae per clump recorded 24 h after introduction to the test apparatus.

behaviors in many tick species (Waladde and Rice 1982). The proximate mechanisms that enable ticks to determine a height at which climbing should cease are unknown. It is possible that larvae of *D. albipictus* have a sense of height, distance traveled, or the length of time since climbing began.

In the wild, numbers of larvae peak on vegetation during the breeding season of moose (Drew and Samuel 1985) (our period 2). During this time, rutting males court females and, in the process, both sexes, but particularly males, cover large areas of potentially tick-infested habitat. In the current study, the greatest number of clumps was found outdoors during period 2.

We are unclear as to the cause of the increase in height of clumps during the latter parts of our study, including the high proportions of clumps found above the shoulder height of moose in late October–early November. In general, numbers and activity of larvae decline in October–November with the onset of Alberta's very cold weather (Samuel and Welch 1991), but temperatures during the current study were mild and well above the 10°C threshold for questing by *D. albipictus* (Drew and Samuel 1985). Winter tick larvae might become more active as length of starvation increases. Camin and Drenner (1978) reported that climbing activity of *H. leporispalustris* larvae increased as starvation progressed. If period 2 is indeed the time during which winter ticks prefer to climb, the behavior of those that were not allowed to climb until periods 3 and 4 may have been influenced by starvation.

Abiotic factors such as daily maximum temperature, maximum relative humidity, or total radiation often affect activity of ticks (reviewed by Sonenshine 1993, also see Loye and Lane 1988). Most larvae outside formed clumps on the shaded (and mostly leeward) east and north sides of rods, apparently to avoid the dislodging effect of wind and desiccation. Drew and Samuel (1985) and Aalangdong (1994) made similar observations at nearby Elk Island National Park. The strongest autumn winds in the region are generally from the northwest and the most persistent winds

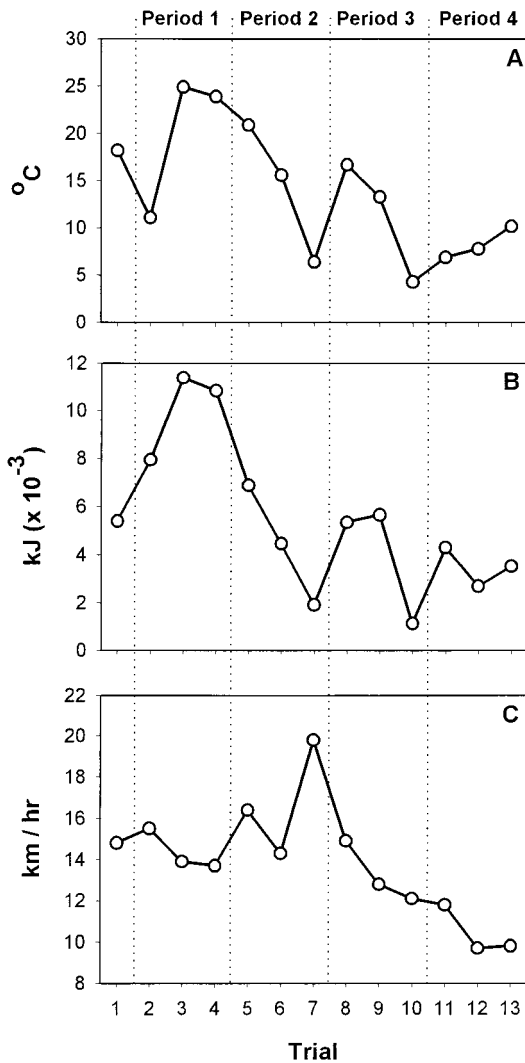


Fig. 5. Weather data recorded during each trial 24 h after tick larvae were introduced to the test apparatus: (A) Daily maximum temperature. (B) Daily total solar radiation. (C) Daily mean wind speed. Vertical dashed line indicates grouping of trials into periods.

blow from the south (Olson 1985). Lees and Milne (1951) felt that wind and sun (in that order) affected the position of adult *I. ricinus* on vegetation. Far fewer winter tick larvae climbed indoors than outdoors, suggesting that there was some proximate environmental factor involved. The outdoor locations had more extreme temperatures than indoors, and although we did not take measurements, the intensity and quality of light must have differed as well. We found no correlations between the variety of abiotic factors we did measure and the climbing activity and clump formation of winter tick larvae outdoors, except between clump height and wind speed. The interaction between abiotic factors and behavior of winter tick larvae appears to be complex and determination of the

proximate mechanisms may require experiments that control and manipulate those factors.

Dermacentor albipictus in central Alberta is near the northern boundary of its range (Samuel 1989), presented with only a brief opportunity for transmission in short, northern autumns (Samuel and Welch 1991). The larval adaptations discussed here (climbing to host-torso level, positioning in shade and leeward, and clumping to decrease water loss) might be critical for transmission in this situation. If the behaviors we observed do reflect local adaptation by the tick, an appropriate test would be to repeat these climbing experiments using *D. albipictus* from an eastern part of the range where white-tailed deer are the only available cervid host (Amerasinghe et al. 1992), and the suitable height for clump formation (our zone 2) would be much narrower.

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