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FACTORS AFFECTING TRANSMISSION OF LARVAL WINTER TICKS, *DERMACENTOR ALBIPICTUS* (PACKARD), TO MOOSE, *ALCES ALCES* L., IN ALBERTA, CANADA

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ABSTRACT: The larval stage of the winter tick, *Dermacentor albipictus*, was studied under field conditions in central Alberta, Canada. Larvae ascended vegetation in autumn, possibly in response to photoperiod. Numbers found by flagging increased from early September to early October and decreased gradually to zero by December. Larvae clumped on the tips of vegetation approximately 1–1.5 m off the ground, and did not exhibit a diurnal, vertical migration. Activity was temperature dependent and no obvious preference of vegetation species for ascension was detected. Transmission of larvae to moose was probably facilitated by synchrony of the larval activity period with the moose breeding season in autumn.

INTRODUCTION

Little is known about transmission of ticks to vertebrate hosts under field conditions. Ticks can respond to odors, vibration, vision, touch, and heat for locating and attaching to hosts, but the relative importance of these stimuli are unclear (see review of Waladde and Rice, 1982). Studies on specific differences in host-seeking behavior of many tick species are recent, and information is scattered throughout the literature (Waladde and Rice, 1982). Larval winter ticks (*Dermacentor albipictus*) ascend vegetation in autumn, apparently in response to one or several environmental stimuli such as frost or photoperiod (Cowan, 1946; Wilkinson, 1967; Wright, 1969a, 1971). Once on the vegetation, larvae clump (Wilkinson et al., 1982) and wait for a passing host.

The winter tick is a one-host tick that usually infests large cervids (see lists of preferred hosts in Bishopp and Wood, 1913; Gregson, 1956; Samuel and Barker, 1979). In Alberta, infestation of moose (*Alces alces*) by larvae usually occurs in autumn. Larvae develop to nymphal and adult stages on moose during winter and early spring; by mid- to late-May, moose are tick-free (Samuel and Barker, 1979; Glines, 1983; Drew, 1984).

From 1977 to 1982, many dead and debilitated moose were found annually in central Alberta (Samuel and Barker, 1979; Samuel and Rippin, unpubl. data). Moose were found with large numbers of ticks and severe, premature, tick-induced loss of winter hair (Samuel and Barker, 1979; Glines, 1983).

This study was initiated in an attempt to better understand the epizootiology of tick infestations on moose in central Alberta. The major objectives were to determine distributional, dispersal, and behavioral patterns of free-living larval winter ticks and how such patterns might influence transmission of larvae to moose.

MATERIALS AND METHODS

Description of study area

The major study area was Elk Island National Park located approximately 40 km east of Edmonton in central Alberta. Elk Island Park is in an aspen parkland ecotone between a grassland and boreal forest biome. The dominant vegetation is aspen (*Populus tremuloides* and *P. balsamifera*) forest interspersed with grassland and black spruce (*Picea mariana*) lowlands. There is a dense understory of beaked hazelnut (*Corylus cornuta*), aspen and wild rose (*Rosa* spp.) (Polster and Watson, 1979), but due

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to high ungulate populations, most shrubs are only 1–1.5 m in height.

Vegetation was classified at each moose carcass site (see below) in the spring of 1981 and 1982 using 1-m^2 plots. Relative density, relative frequency, and importance values were calculated for each plant species following methods of Cottam and Curtis (1956).

Collection of weather data

Temperature and relative humidity were recorded continuously in three habitat types (bog, aspen forest, and grassland) in the Park from July to December 1981 and from April to December 1982 using hygrothermographs in Stevenson screens set at ground level.

Movement and activity of larval ticks

Carcasses of moose that were found dead or shot in late winter had large numbers of *D. albipictus*, including engorged females, and were assumed to be good locations for finding larvae the following autumn. Locations of carcasses were grouped into six habitat types (bog, dry grassland, wet grassland, open canopy aspen, dense canopy mature aspen, and dense canopy immature aspen) based on a subjective evaluation of relative density and importance of plant species in the canopy stratum (see Drew, 1984, for details). Seven and five carcasses were located and marked from February to May 1981 and 1982, respectively.

Vegetation around carcasses and along game trails was sampled for larvae in autumn 1981 and 1982, using 0.5-m^2, white flannel suspended from a wooden pole. Flagging was done weekly from 7 September to 24 December 1981 and from 16 August to 20 December 1982. In addition, all carcass sites were flagged twice the following spring to see if any larvae had survived winter.

While standing on the carcass remains, vegetation up to 0.5 m from the carcass was flagged using one flannel; vegetation 0.5–1 m from the carcass was flagged using a second flannel. Each flannel was placed in a labelled, plastic bag and taken to the laboratory. There, all larvae were counted by aspirating them into a small, glass vial using a vacuum apparatus.

Single 20-m sections along six game trails were flagged by walking down the trail with the flannel on one side, then walking back with the flannel on the other side. Vegetation within 0.5 m of both sides of each trail was flagged. Flannels were treated as described above.

Efficiency of the flagging technique was assessed by seeding each of three sites (bog, aspen forest, and grassland) in the Park with 5,000 laboratory-reared larvae on 11 October 1982. Each site was flagged 10 times from 18 October to 20 December 1982.

Larval *D. albipictus* reared in the laboratory were counted, dyed with fluorescent pigments, and released onto a series of 1-m^2 vegetation plots on the roof of the Biological Sciences Center at the University of Alberta in autumn 1981 and 1982 to observe behavior patterns. Larvae were released onto three vegetated plots with progressively taller vegetation, 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 reaction to light. All plots were observed every 4–6 hr for the first week after release of larvae and one to three times daily thereafter until the experiment was terminated 81 days post-release.

The height of nine to 38 arbitrarily-selected larval clumps around each carcass site sampled for larvae in Elk Island National Park was measured in October 1981 and 1982. 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.

RESULTS

A total of 2,394 larvae was recovered by flagging the three sites (each seeded with 5,000 larvae), giving an average 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 assumed to be similar in efficiency. Because only a small proportion of the larvae around carcass sites were likely removed by the flagging technique, it was assumed that the results at carcass sites reported here reflect actual changes in larval numbers under field conditions rather than removal due to repetitive sampling at the same site.

Larval *D. albipictus* were collected from vegetation at all seven carcass sites in 1981 and at one of five carcass sites in 1982. Although there were large variations between numbers of larvae flagged at each carcass site, the overall pattern was consistent (Fig. 1): a rapid increase in numbers of larvae in early- to mid-September

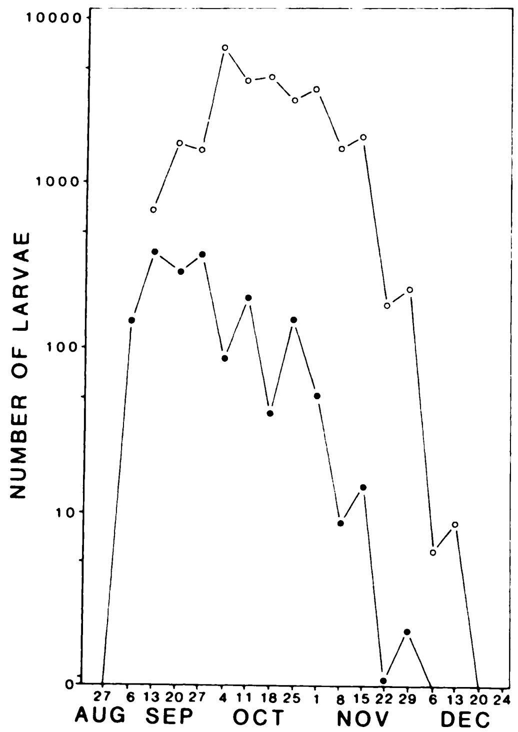

FIGURE 1. Changes in mean numbers of larvae of *Dermacentor albipictus* collected by flagging around moose carcasses at Elk Island National Park, Alberta, 1981 (O) and 1982 (●). Larvae were collected from seven carcasses in 1981 and one carcass in 1982.

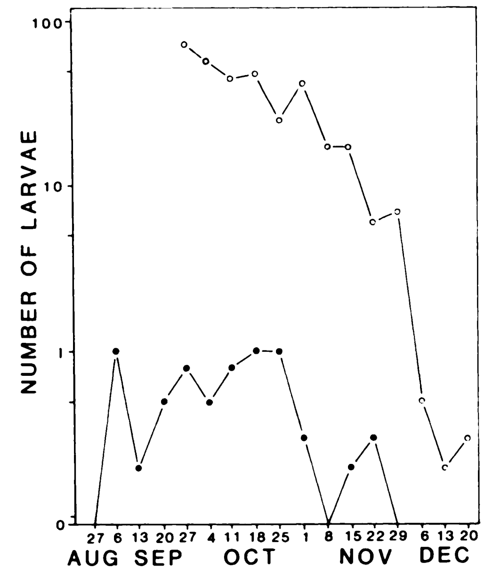

FIGURE 2. Changes in mean numbers of larvae of *Dermacentor albipictus* collected by flagging along six game trails at Elk Island National Park, Alberta, 1981 (O) and 1982 (●). The same trail sites were used in both years.

was followed by a rapid decline in numbers by mid-November. Numbers of larvae were at or near zero by late December and only a few larvae were seen on vegetation until mid-February. No larvae were found by flagging carcass sites in the spring of 1982 or 1983 indicating that larvae survived a maximum of about 3–4 mo, under field conditions.

Numbers of larvae flagged along game trails were much lower than at carcasses (Fig. 2), but the general decreasing trend in larval numbers was similar. Only 39 larvae were collected in 17 wk of sampling along game trails in 1982, compared to a total of 2,005 flagged in 1981.

Larvae on the roof of the Biological Sciences Center and in Elk Island Park consistently ascended to the maximum height of available vegetation and supports, although no preferred height was observed. Larvae aggregated in clumps on the tips of vegetation (Fig. 3). Clump height varied from 4 cm to 4 m off the ground, usually at or near the tips of the vegetation. 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 picked up by a host, blown off by the wind, or died.

Due to small sample sizes of vegetation with and without larval clumps in all but the aspen habitat in Elk Island Park, results of vegetation preferences of larvae were inconclusive. The mean height of clumps of larvae was very close to the mean height of the available vegetation (Table 1). Larger numbers of clumps were found on grass, possibly reflecting the high importance value rank of grass in the

FIGURE 3. A clump of larvae of *Dermacentor albipictus* on beaked hazelnut (*Corylus cornuta*) in Elk Island National Park, Alberta. (Photo by M. Pybus.)

shrub/herb layer. The largest clumps were found on aspen in spite of its relatively low importance value rank (Table 1), possibly indicating an attraction to or preference for this species of vegetation.

The week-to-week increases and decreases in the numbers of larvae flagged around carcasses in both years appeared related to ambient temperature on the day of sampling. There was a positive correlation between temperature at the time of flagging and numbers of larvae flagged for five of the eight carcass sites (Pearson's product moment, $r > 0.64$, $P < 0.05$). 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.

Results of over 350 observation periods indicated that activity of larvae 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, activation occurred 2–3 min following exposure to human skin. At temperatures below −8 C, larvae became active only after exposure to human skin for 15–60 min.

For the first 7–10 days after release, larvae in experimental plots avoided high light intensities. Most larval clumps (>90%) were on the shaded side of upright stems and artificial supports, or on the underside of horizontal leaves and branches. The clumps moved continuously 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 Elk Island Park behaved similarly.

DISCUSSION

Larval *D. albipictus* in Elk Island National Park were available for transmission to moose from early September to mid-November, although they did not ascend vegetation until about 2 wk after hatching in mid-August and early September (Drew, 1984). In contrast, most literature sources refer to a summer hatch and a delay in host-seeking by larval winter ticks 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, 1926–1927), an inactive state (Howell, 1939), quiescence (Drummond, 1967), and diapause (Wright, 1969b). "Quiescence" is probably the best designation because the described delay has not been shown to be due to the lack of a growth hormone, and it appeared related to local weather factors. (For a definition of quiescence and other terms, see Wigglesworth 1970, 1972; Belozerov, 1982; Chapman, 1982; Saunders, 1982.) The possibility of a genetically determined diapause must not be excluded. The quiescent period of larval *D. albipictus* under field conditions varies greatly with geographical location: 4–7 mo

TABLE 1. Height and size of clumps of larval *Dermacentor albipictus* in the aspen habitat type in Elk Island National Park, Alberta, 1981.

Vegetation	Importance value rank[a] (range 1–14)	Number clumps measured	Clump: No. of larvae $\bar{x}$	Clump: No. of larvae Range	Clump: Height (cm) $\bar{x}$	Clump: Height (cm) Range	$\bar{x}$ height of vegetation without larval clumps (cm)
Aspen (*Populus* spp.)	9	31	221	10–1,000	131	58–400	140
Grass (Graminae)	4	36	99	10–500	61	20–100	77
Rose (*Rosa* spp.)	2	24	173	50–700	82	57–132	86
Beaked hazelnut (*Corylus cornuta*)	7	10	208	50–1,000	106	75–130	108
Raspberry/blackberry (*Rubus* spp.)	7	5	147	25–200	86	34–160	106

[a] Importance value is the sum of relative density and relative frequency. Fourteen plant species were sampled, the most important species being assigned the rank of 1 (see Drew, 1984, for details).

in California (Howell, 1939), 4–5 mo in Oklahoma (Patrick and Hair, 1975), 3–6 mo in Texas (Bishopp and Wood, 1913), 2–3 mo in British Columbia (Wilkinson, 1967), and about 2 wk in Alberta (Drew, 1984).

The activation of larval winter ticks after the quiescent period has been attributed to many factors including the advent of frost in autumn (Cowan, 1946), a complex interaction between photoperiod and above-freezing soil temperatures (Wilkinson, 1967), and photoperiod alone (Wright, 1969a, 1971). Wright (1969b) was able to terminate "diapause" in larval *D. albipictus* by immersing them in an analog of molting hormone (alpha-ecdysone). 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. Photoperiod is one possible explanation for the constancy in initiation of larval activity (early September) in both years of this study.

Photoperiod may partially explain the similarities between 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 differences between ascension dates found by Patrick and Hair (1975) and that reported here. 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. 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 to determine the importance and mechanism by which photoperiod might cue larval activation.

Almost all larvae clumped at the tips of the vegetation and were available for transmission to moose continuously from September to November except for periods when temperatures were below 0 C. Due to the overbrowsed condition of the vegetation in Elk Island Park, most larval clumps were about 1 to 1.5 m above the ground (Table 1). This might be an optimal height for host acquisition, being approximately chest high on moose or wapiti (*Cervus elaphus*).

The clumping of larval winter ticks on vegetation is probably an active, 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 may be due to an aggregation substance, possibly a pheromone (Sonenshine et al., 1982).

Clumping may have several adaptive advantages including protection from desiccation and enhancement of host acquisition. It may ensure that more larvae would be able to attach when a host passed by. Although 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.

Moose behavior may also enhance host acquisition by larvae. Moose concentrate in particular areas during calving, rutting, and late winter; the same area can serve all three functions (Van Ballenberghe and Peek, 1971; LeResche, 1972; Phillips et al., 1973). If "ticky" moose have similar behavior and use the same areas in late winter (=when engorged females are dropping from moose) and autumn, the probability of encountering clumps of larvae in these areas in autumn would be increased. Therefore, having clumps of larvae at optimal heights in optimal locations 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; Gregson, 1951; Wilkinson, 1953, 1961; Rothschild, 1965; Samuel and Trainer, 1971).

The lack of a diurnal, vertical migration by larval *D. albipictus* presents an apparent paradox between success of transmission and desiccation. Although many species of ticks 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 vegetation (Lees and Milne, 1951; Camin and Drenner, 1978; Yosida, 1979; Knulle and Rudolph, 1982).

Almost all ticks have some water conserving adaptations and can survive desiccation for long periods of time (see review of Knulle and Rudolph, 1982). However, the extent of development and utilization of these adaptations is dependent on climatic factors in the habitat in which the tick exists (Knulle and Rudolph, 1982). Unfed ticks have three major means of regaining body water: migration to the soil duff; uptake of water vapor from the atmosphere; and imbibition of water from dew or rain droplets (Knulle and Rudolph, 1982). The lack of a diurnal, vertical migration by larval winter ticks may be due to either highly developed water conservation mechanisms, or to a well developed ability to extract water from the atmosphere when relative humidity levels peak at night.

Unlike some studies (McCulloch and Lewis, 1968; Lewis, 1970; Rechav, 1979), horizontal dispersal of larval winter ticks appeared minimal. Most larvae seemed to ascend vegetation in the immediate vicinity of the hatching site, therefore, the distribution of larvae was assumed to be dependent directly on the distribution of engorged females. Similar findings have been reported by Lees and Milne (1951) for *Ixodes ricinus* and Bishopp and Hixson (1936) for *Amblyomma 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 decline in larval numbers flagged in autumn around moose carcasses (Fig. 1) may relate to the general decline in daily temperatures that occurred. The abrupt decline in mid-November from temperatures averaging over 0 C to temperatures averaging below 0 C (Drew, 1984) appeared to have a cause/effect relationship to the marked decline in larval numbers flagged around carcasses in both 1981 and 1982.

The numbers of larvae flagged at each carcass in autumn were probably related to the date each moose died the previous winter–spring. The prevailing weather conditions at the time of death, particularly the presence of snow, would determine survival rates of engorged females (Drew, 1984; Drew and Samuel, unpubl. data). Date of death would also influence the numbers of engorged females per moose; more being present in April and May than any other time (Glines, 1983; Drew, 1984; Samuel, unpubl. data). The importance of carcass sites to the transmission of winter ticks is unknown.

Preliminary results suggest a potential relationship between numbers of larvae flagged in autumn along trails and numbers of ticks per moose collected the following winter. In winter 1982, following an autumn when numbers of larvae flagged along trails were high, tick numbers averaged slightly over 40,000 per moose, the highest found since monitoring of ticks in the Park began in 1978 (Samuel, unpubl. data). In winter 1983, following an autumn when few larvae were flagged, tick infestations per moose averaged about 20,000 (Samuel, unpubl. data).

Moose were probably at continuous risk to infestation by *D. albipictus* for several months in autumn, because they move approximately 1 km per day then (Edwards and Ritcey, 1956; Knowlton, 1960; Van Ballenberghe and Peek, 1971), and larvae are active. Although peak exposure is early October, the length of exposure period appears dependent on temperature declines in autumn. Early frosts and snowfalls could shorten the exposure period by decreasing activity and increasing mortality of larvae.

Peak activity of larvae occurs during 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 travel farther than females during the rut (Phillips et al., 1973; Roussel et al., 1975), which may explain why males average twice as many ticks per individual as females ($\bar{x}$ = 45,341 and 21,120 for 18 males and 24 females, respectively; Samuel, unpubl. data). This association may be coincidental, but Nelson et al. (1975) state that, for unresolved reason(s), males of many host species carry a larger population of ectoparasites than females.

Results of this study indicate that an intricate relationship exists between weather, moose, and larval winter ticks. The system is obviously fine-tuned because in Alberta, near the northern limit of this tick's range, most if not all moose are infested (Samuel and Barker, 1979).

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BOOK REVIEW . . .

Color Atlas of Diseases of the Domestic Fowl and Turkey, C. J. Randall. Iowa State University Press, 2121 South State Avenue, Ames, Iowa 50010, USA. 1985. 116 pp. $27.50 US.

In the preface the author states that the "purpose of this atlas is to provide the diagnostician with photographs of the main post-mortem and histopathological features of common diseases in the domestic fowl and turkey. The atlas does not aim to cover the other procedures that may be required to confirm a diagnosis." The book was designed to be used in connection with textbooks of poultry diseases such as Hofstad et al. (1978, Diseases of Poultry, 7th Ed., Iowa State Univ. Press).

There are 311 color photographs which cover 12 bacterial diseases, 14 viral diseases, 3 neoplasias, 3 mycotic diseases, 9 parasitic diseases, 5 nutritional deficiencies and metabolic disorders, 12 diseases of uncertain or unknown etiology, and 10 miscellaneous conditions. Most of the photomicrographs are of tissue sections which have been stained with hemotoxylin and eosin.

The quality of the photographs is excellent. Although this atlas deals with diseases of domestic poultry, those people working on diseases of wild gallinaceous birds will find this book very useful. It is well worth the price.

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