

RECRUITMENT OF WINTER TICKS (*DERMACENTOR ALBIPICTUS*) IN CONTRASTING FOREST HABITATS, ONTARIO, CANADA

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ABSTRACT: Recruitment of winter tick larvae (*Dermacentor albipictus*) was studied in a forest opening and a closed canopy deciduous forest to evaluate their potential as sources of tick infestation to moose (*Alces alces*). Engorged female ticks were set out in early May at each site and monitored to measure the proportions of females producing larvae and the number of larvae recruited per g of surviving female. Recruitment was higher in the forest during the hotter, drier summer of 1983, primarily due to fewer engorged females producing larvae in the opening, and was much higher (>2 x) in the opening during the cooler, damper summer of 1984. Recruitment in the field was 20–40% of that under laboratory conditions. Desiccation of eggs and/or larvae was the probable cause for the annual variation in recruitment in the opening. Most larvae were recruited earlier in the opening than in the forest site. Neither weight nor date of detachment of engorged female ticks influenced when larvae first ascended vegetation. Weather, especially temperature, and site structure and composition affect abundance of the free-living stages of the winter tick and larvae available for transmission to moose. Open sites should support more winter tick larvae than densely forested sites except in years of particularly hot and dry weather.

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The overall impact of winter ticks (*Dermacentor albipictus*) on moose (*Alces alces*) populations varies annually (Samuel 2004). Understanding the reasons for this variation is key to predicting when and in what habitats moose are most likely to acquire winter ticks. Survival of eggs and larvae of ixodid ticks are affected most markedly by desiccation (Sonenshine 1970), and since temperature and moisture vary annually, reproductive potential of ixodid ticks can also vary annually within the same habitat (Patrick and Hair 1979, Fleetwood et al. 1984). Production and survival of winter tick eggs and larvae from wapiti (*Cervus canadensis*) have been studied in 2 habitats in Oklahoma, USA

(Patrick and Hair 1975), and from moose in a variety of habitats in central Alberta, Canada (Drew and Samuel 1986, Aalangdong et al. 2001). Objectives of this study were to establish if adult females, eggs, and larvae of the winter tick could survive in 2 contrasting forest habitats in Ontario, Canada, and to document factors related to variation in recruitment between years and habitats.

STUDY AREA

Two study sites 13.3 km apart in Algonquin Provincial Park, Ontario were selected for their contrasting habitats: 1) a forest opening and 2) a closed canopy deciduous forest. The opening site was an old lumber camp

(45° 42' 13" N, 78° 15' 9.5" W) with ground vegetation <0.3 m high and comprised of scattered grasses, sweet fern (*Comptonia peregrina*), bracken (*Pteridium aquilinum*), and blueberry (*Vaccinea* sp.); trees were limited to red pine (*Pinus resinosa*) and white spruce (*Picea glauca*) <3 m high and present in 11% of plots. The deciduous forest site (45° 35' 6" N, 78° 18' 53" W) was on a northeasterly aspect sloping away from the summer sun, with a closed canopy dominated by sugar maple (*Acer saccharum*) with scattered white birch (*Betula papyrifera*). Sub-canopy vegetation was limited and ground vegetation was predominantly sugar maples 1–1.5 m high.

METHODS

Weather data were collected from “An Historical Climate Analysis, version 2.2” which uses latitude and longitude, Environment Canada data, and topographical source data to calculate location specific weather (Cross et al. 2012). Specific weather data (e.g., temperature, precipitation, snow accumulation) were recorded occasionally at the study sites.

We attempted to minimize and control for the influence of outside factors that could affect the outcomes of live specimens. Specifically, we:

- 1 divided into 2 treatment groups winter ticks that detached on the same date from moose with similar exposure history and infestation level to account for immunocompetence that can suppress fecundity in ticks (McGowan et al. 1980, 1981, Chiera et al. 1985),
- 2 allocated similar-sized engorged ticks between treatment groups to account for the relationship between weight and fecundity (Drummond et al. 1969, Addison and Smith 1981, Drew and Samuel 1987, Addison et al. 1998), and further, calculated fecundity relative to weight,
- 3 used control plots and documented dissemination from points of deposition to account for ingress and egress of adult female and larval ticks,

- 4 assumed that losses to predation and disease were constant (Addison et al. 1989, Tuininga et al. 2009), and
- 5 used sites where the height of vegetation conformed with the known ascension height of winter ticks (0.5–1.9 m; Drew and Samuel 1985, McPherson et al. 2000).

Definitions

The following terms are used in the paper:

- 1 Reproductive efficiency index (REI) is the number of eggs produced per g of engorged adult female tick (EF) (Drummond and Whetstone 1970).
- 2 Larval efficiency index (LEI) is the number of larvae recovered from a plot per g of EF placed on that plot, and was calculated only for plots from which larvae were recovered.
- 3 Flagging is the action of dragging flannel sheets over vegetation to sample larvae available for transmission.
- 4 Recruitment is a measure of tick larvae available for transmission by flagging and is comprised of both LEI and proportion of EFs producing larvae.
- 5 Season of transmission is the time from first to last collection of larvae by flagging.
- 6 Minimum free-living period is time (d) from detachment of an EF to first recovery of larvae from that EF by flagging.
- 7 Vapor pressure deficit (VPD) is a measure of the difference (or deficit) between the pressure (mm Hg) exerted by the moisture currently in the air and the pressure at saturation.

Engorged Female Ticks (EFs)

Detached EFs were collected on 1–20 April, 1983 and 15 March–27 April, 1984 from captive moose experimentally infested with ticks (see McLaughlin and Addison 1986). Prior to placement in the field, they were maintained at ambient temperature within cardboard boxes containing moist sand and soil overlaid with leaves. A total of 100 EFs were marked on the abdomen with nail polish (Revlon Nail Enamel, Ottawa, Canada K1G 3N1), and one set of 50 was placed at flagged locations in the

forest and opening sites in early May. Their dispersal distances were measured in early July.

An egg group (3.775 g) equivalent to ~54,000–63,000 eggs (see Addison et al. 1998) was deposited at a single point in 2 grass plots in the opening site. From point of deposition, concentric 1-m wide rings were flagged 4 m outward to measure dispersal of larvae in late September through mid-October.

Fecundity and Hatching

Forty EFs were selected at random and each placed in a 2 cm² cell within wood frame trays approximately 3 cm deep, enclosed on top and bottom by insect screening. One tray was placed on the soil surface and covered with ground vegetation in each study site in early May. Eggs were collected from individual EFs and counted weekly from 8 June until deposition ended.

Fifty EFs were placed in each of 6, 60 cm² wooden trays with fine screening on top and bottom. One tray was placed in each of 3 locations within each study site during mid-May and examined weekly to document initial presence of larvae.

Larval Recruitment

In 1983 (5–7 May), 453 and 451 EFs were placed on the ground singly, 5–10 m apart, in the opening and forest sites, respectively. Numbered plastic tape identified each plot with date of detachment, moose of origin, and weight of the EF; placement location was the center of a 2.5 m radius plot that was the source of data for larval recruitment. In 1984 (3–4 May), 213 and 206 EFs were placed similarly in the opening and forest sites, respectively. Control locations (without ticks) were also established - 10 in the opening and 8 in the forest site.

Plots were flagged (sampled) with white, flannel sheets (2.3×2.6 m) every 9–13 (1983) and 11–15 (1984) days from August

until after snowfall (3–22 November). One end of the flannel sheet was wrapped around a stick (2.4×0.05×0.02 m) until about 30 cm of the sheet was rolled in. The plot was flagged by dragging the sheet over the vegetation such that no person walked within 2.5 m of the plot center; the center area (~0.5 m out from the center point) was flagged once separately.

The sheet was examined and if few larvae were present, they were counted, killed, and removed. If numerous larvae were collected, the sheet was folded by 2 people, bagged, and labeled. Larvae were subsequently counted as they were evacuated (–40 kPa relative pressure) from the sheet. Sheets were washed and dried in an electric dryer prior to reuse.

In 1983, all plots were flagged and larvae counted through to the end of the season. Plots were considered positive (i.e., EFs had survived) if >10 larvae were recovered. In 1984, plots were identified as positive or negative in mid-September and a random subsample of positive plots was used for further measurements of total larval count. Survival was measured by flagging these and the remaining plots and categorizing them positive or negative.

Data Analysis

Placement of EFs on plots and subsequent flagging of plots to establish recruitment occurred in both 1983 and 1984. Timing of incubation of eggs, presence of larvae on control plots, and dispersal of EFs and larvae were studied only in 1984.

The R statistical package (R Core Team 2013) was used to analyze data on eggs, REI, and duration of the non-parasitic period. Egg production and REI data were not normally distributed (Shapiro-Wilk Test) and variances were not homogenous. Since transformations did not normalize data, the Mann-Whitney-Wilcoxon test was used to test for differences in number of eggs

produced and REI between habitats. Duration of the non-parasitic period was tested for normal distribution with the Shapiro-Wilk test. Transformations harmonized the variances (Bartlett's test) and while normal distributions were not realized, the consequences of this were acceptable to use factorial ANOVA (Glass et al. 1972, Harwell et al. 1992, Lix et al. 1996). Three-way contingency tables and Chi-square tests were used to evaluate frequency of positive plots between years and habitats (Zar 1982). Square root transformation was applied to the number of larvae produced per g for EFs that produced larvae (LEI); this transformation stabilized the variance (Bartlett's test) and normalized the distribution (Kolmogorov-Smirnov test). Data for the first appearance of larvae on vegetation, size of EFs, and date of detachment of EFs could not be normalized through transformation because of the discontinuous nature of the sampling protocol both years: 9–13 and 11–15 days in 1983 and 1984, respectively (Fig. 4, 5). Consequently, scatter diagrams were used to evaluate possible relationships.

RESULTS

Average monthly temperature and precipitation varied annually (Table 1). May was wetter, June and July (the period of

egg-laying and incubation) were warmer and drier, and September (period of larvae ascending) was warmer and wetter in 1983 than 1984. Temperature was intermittently low and snow fell late in the experiment. For example, in 1983 the morning air temperature at the forest site was $-6\text{ }^{\circ}\text{C}$ and the ground was solid with heavy frost on 15 October, 10–15 cm of snow accumulated in the forest on 8 November and was gone by 10 November, and finally 10–15 cm of snow permanently covered the ground on 22 November.

Dispersal and Fecundity

Mobility was limited for both EFs and larvae. In the opening, 44 of 45 EFs were recovered within 67 cm, and in the forest 41 of 42 were recovered within 34 cm of the site of deposition. In the opening, 98.5% of 26,485 larvae moved <2 m from the site of egg deposition. A similar number of EFs held in trays laid eggs in the opening (64%) and forest (70%) in 1984. However, EFs in the opening laid more ($P < 0.05$) eggs (median = 6226) than in the forest (median = 3632), and the REI in the opening (median = 8150) was greater ($P < 0.05$) than that in the forest (median = 4620). Further, EFs in the opening completed ovipositing on 27 July, a month earlier than in the forest (30 August).

Larval Recruitment

Larvae hatched about 2 weeks earlier in the opening (4 August) than the forest (17 August) in 1984, were recruited earlier in the opening than the forest both years, but not until 2–4 weeks post-hatch in 1984 (Table 2, Fig. 1). Most opening plots became positive for larvae later in 1983 than 1984 (Fig. 1); in contrast, forest plots were positive at the same time both years (Fig. 1). Approximately 80% of all larvae were recruited in the opening by late September, about 2 weeks prior to the forest (Fig. 2). Minimal numbers

Table 1. Average monthly temperatures and precipitation at opening and forest study sites in Algonquin Park, Ontario, 1983–1984.

Month	temperature ($^{\circ}\text{C}$)		precipitation (mm)	
	1983	1984	1983	1984
May	8.8	9.1	167.5	116.3
June	16.8	16.6	51.9	83.7
July	19.6	18.0	62.4	102.8
August	18.8	18.7	97.8	96.6
September	14.7	11.7	104.2	87.7
October	6.3	8.5	112.9	64.1

Table 2. Recovery of *Dermacentor albipictus* larvae from contrasting habitats of the Great Lakes – St. Lawrence forest ecosystem, Algonquin Park, Ontario, 1983–1984.

	Open Field		Deciduous Forest	
	1983	1984	1983	1984
1 st Larvae Flagged	Sept 6	Aug 28	Sept 13	Sept 18
% Engorged Females (EFs) with Larvae	38 (n = 453)	88 (n = 193)	67 (n = 450)	85 (n = 196)
LEI ¹ for EFs with Early ² Larvae	1502 ± 1186 (n = 71)		1520 ± 1112 (n = 50)	
LEI for EFs with Late ³ Larvae	346 ± 506 (n = 19)		868 ± 711 (n = 19)	
Total LEI	1258 ± 1176 (n = 90)	3214 ± 1734 (n = 49)	1340 ± 1054 (n = 69)	1463 ± 1315 (n = 50)

¹Larval Efficiency Index = number of larvae/gram of engorged female from which larvae recovered).

²Larvae first flagged in September.

³Larvae first flagged in October.

of larvae were collected during flagging in early to mid-November both years (Figs. 2, 3). In the opening, <13 larvae were recovered in 9 of 10 control plots; 1 plot yielded 5,283 larvae. In the forest, 2 control plots had <10 larvae and 6 plots had none. A higher proportion of EFs produced larvae in the forest than the opening in 1983 ($P < 0.05$); no difference was found in 1984 ($P > 0.05$) (Table 2). At both sites fewer plots yielded larvae in 1983 ($P < 0.05$) (Table 2).

Recruitment of larvae ranged from 10–7,347 larvae per surviving EF. The mean LEI was similar ($P > 0.05$) both years in the forest; however, the LEI in the opening was higher (>2x) in the cool, wet summer of 1984 than the hot, drier summer of 1983, as well as both years in the forest ($P < 0.05$) (Table 2, Fig. 3). In both habitats in 1983, LEI from EFs from which larvae were available in September (early samples) was higher ($P < 0.05$) than from EFs from which larvae were first recovered in October (late samples) (Table 2, Fig. 3).

Minimum Free-Living Period

The minimum free-living period ranged from 122–215 days (n = 699, $\mu = 162$).

Effects of habitat, year, and the interaction between habitat and year on the minimum free-living period were significant ($P < 0.05$), but neither weight nor date of detachment of EFs influenced duration of the free-living period (Fig. 4, 5).

DISCUSSION

Winter tick larvae were available in both contrasting habitats, hence, are likely available for transmission in most terrestrial habitats frequented by moose in the Great Lakes – St. Lawrence forest ecosystem. Annual differences in fecundity and recruitment of larvae and between habitats reflected the influence of weather, habitat structure and composition, and their interactions. Many tick studies have documented higher temperature, lower RH, and higher VPD in open (e.g., fields) compared to forest habitats during summer; e.g., in Alberta (Aalangdong et al. 2001), Oklahoma (Patrick and Hair 1975), Virginia (Sonenshine 1970), east-central Texas (Fleetwood et al. 1984), and Connecticut (Bertrand and Wilson 1996). Wind also has a drying effect, open habitats being usually drier than closed habitats (Schütte and King 1965), and sites with

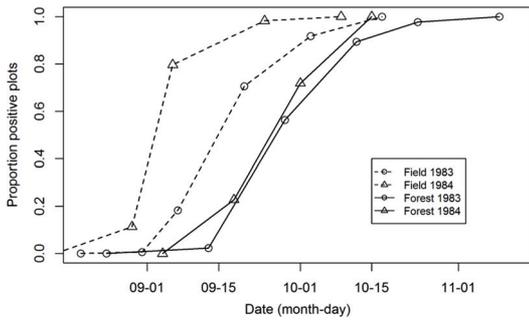


Fig. 1. Accumulation of tick plots with larvae of *Dermacentor albipictus* in opening and forest habitats, Algonquin Park, Ontario, autumn 1983 and 1984.

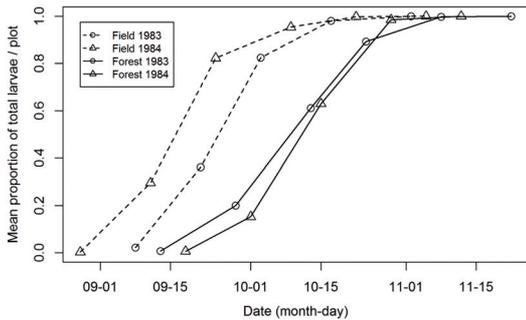


Fig. 2. Proportion of total seasonal recruitment of larvae of *Dermacentor albipictus* acquired during individual sampling periods in opening and forest habitats, Algonquin Park, Ontario, autumn 1983 and 1984.

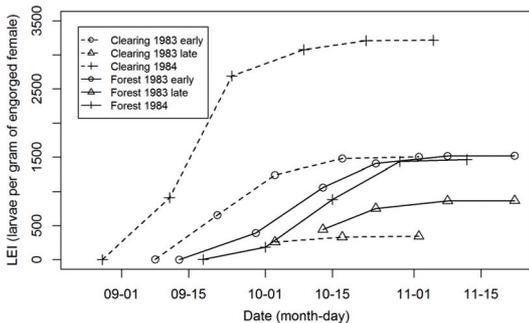


Fig. 3. Larvae per gram of engorged female (LEI) *Dermacentor albipictus* recruited from opening and forest habitats, Algonquin Park, Ontario during early and late autumn 1983 and autumn 1984.

aspect towards the summer sun being hotter and drier (Londt and Whitehead 1972).

We had no weather data at the microsite level (i.e., in the duff layer where eggs and larvae reside). However, because microsites in open habitats have higher temperature, lower relative humidity (RH), and higher wind speed (Londt and Whitehead 1972, Daniel et al. 1977, Daniel 1978), we assumed that our flat opening had lower RH, and higher temperatures, wind speeds, and vapor pressure deficits (VPDs) at the microsite level than the forest habitat with dense canopy cover and northeast sloping aspect.

Weather and Desiccation

Both eggs and larvae lose moisture under conditions of VPD, with temperature the main influence on vapor pressure. Desiccation of eggs is detrimental because eggs cannot reabsorb water even at high RH (Rechav and Maltzahn 1977). Desiccation of eggs (*Dermacentor variabilis*) occurred when RH was reduced 6–8 h daily, fewer eggs hatched at 85% than 95% RH (Sonenshine and Tigner 1969), and weight and hatchability of *Boophilus decoloratus* eggs were reduced at lower RH (Rechav and Maltzahn 1977). High VPD is correlated positively with weight loss in *Boophilus microplus* and *B. annulatus* eggs, with a strong negative relationship between weight loss and percent hatched (Teel 1984). The ~50% lower recruitment of larvae in the opening in 1983 versus 1984 presumably reflected higher desiccation and mortality of eggs during oviposition and incubation in the hotter and drier June and July of 1983.

Desiccation also threatens tick larvae (Knülle 1966). For example, survival of *Amblyomma hebraeum* larvae dropped precipitously at 70% RH compared to higher RHs (Londt and Whitehead 1972), *Ixodes ricinus* larvae died sooner in open, grassy than in forest habitats (Daniel et al. 1977), and *A. americanum* larval survival was shorter

(10–19 d) in meadow than forest habitat (33–106 d) in Oklahoma (Patrick and Hair 1979).

Incubation of winter tick eggs occurs more rapidly at higher than lower temperatures (Addison et al. 1998). In 1984, larvae first appeared in early August and presumably earlier in 1983 given the hotter June and July. Thus, although desiccation in July

1983 may have impacted larval survival, the higher average monthly September temperature (3 °C) than in 1984 may also have contributed to reduced larval survival and recruitment in 1983. Overall desiccation of larvae may have been moderated by higher precipitation in September 1983 and the relatively lower VPD associated with cooler weather in late August and September. We conclude that reduced recruitment of larvae due to desiccation in the opening in 1983 likely had a minimal role in overall reduced LEI, particularly relative to desiccation of eggs.

Fecundity

While the reduced proportion of EFs with larvae in the opening in 1983 could be attributed to higher desiccation and mortality of eggs and larvae, it is possible that high mortality occurred in EFs prior to egg-laying in the hotter and drier June and July of 1983. In 1984, the REI values in cells within the forest site were ~50% lower than in the opening; in contrast, Drew and Samuel (1986) reported similar REI values for EFs in open and closed habitats. In 1984, the REI values in the opening were similar (median = 7538) to those produced under laboratory conditions ($\mu = 7097\text{--}9443$) (Addison et al. 1998), indicating that conditions in the opening were highly favorable for egg production and more so than at the forest site (May mean monthly temperature of 9.1 °C) where the microsite temperature was presumably lower. Egg production was also lower at 15 °C than at 20 and 25 °C in *Rhipicephalus sanguineus* (Sweetman 1967). In general, it is anticipated that overall fecundity of EFs would be lower in cooler than warmer habitats in northerly parts of winter tick range, that more open habitats are the likely nidus for transmission in cooler summers, and that fecundity might be correlated with latitude within winter tick range.

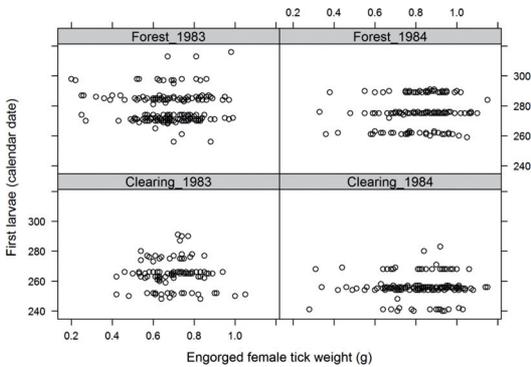


Fig. 4. Scatter gram of weight of detached engorged female *Dermacentor albipictus* versus first date of appearance of larvae on vegetation in opening and forest habitats, Algonquin Park, Ontario, autumn 1983 and 1984.

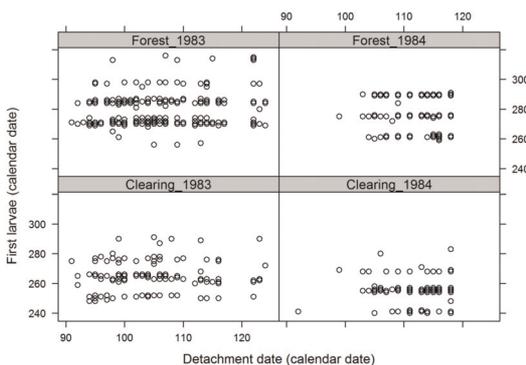


Fig. 5. Scatter gram of date of detachment of engorged female *Dermacentor albipictus* from moose versus first date of appearance of larvae on vegetation in opening and forest habitats, Algonquin Park, Ontario, autumn 1983 and 1984.

Rate of Development

Oviposition occurred earlier in the opening than in the forest. This is consistent with earlier oviposition by winter ticks at 24 °C than at 20 °C under laboratory conditions (Addison et al. 1998) and oviposition of other species of ticks occurring more quickly in open field than in forested sites (Daniel et al. 1977, Dusbabek et al. 1979, Patrick and Hair 1979, Koch 1984). Incubation of winter tick eggs is also accelerated at higher temperatures (Addison and Smith 1981, Addison et al. 1998), hence, the accelerated incubation in the opening as compared to the forest was likely due to higher microsite temperatures. As with earlier oviposition, this could have contributed to the earlier appearance of larvae in the opening than in the forest in both years. Similarly, the incubation period for *D. albipictus* in Alberta was shorter in an open grassland than in an aspen forest (Drew and Samuel 1986), and shorter incubation periods in open fields as compared to forests have been reported for *A. americanum* in Oklahoma (Patrick and Hair 1979) and *D. reticularis* in Slovakia (Dusbabek et al. 1979).

Recruitment of Larvae

LEI, one measure of recruitment, was based only on those EFs that produced larvae. Total recruitment also is affected by the proportion of EFs producing larvae. The LEIs in 1983 and in the forest in 1984 were <20% of the REIs of egg-laying EFs in laboratory conditions (see Addison et al. 1998) indicating about 80% attrition of the maximum potential recruitment from EFs producing larvae; the 1984 LEI in the opening was ~40% of the maximum potential. Total recruitment in 1984 was higher at both sites, particularly in the opening where twice as many plots (EFs) were productive compared to 1983. Conversely, total recruitment in 1983 was highest in the forest habitat where 29% more EFs produced larvae. These results are consistent with the

hypothesis that weather and ground conditions are primary influences on which habitats have highest potential to contribute viable larvae in any given year.

No compensatory increased production of larvae was observed from plots not producing larvae until late in the season. Thus, earlier ascent onto vegetation should be a major advantage if increased availability (time) for transmission to moose is a primary selective advantage; however, desiccation of larvae is also more likely in warmer weather characteristic of earlier transmission in early September.

Winter tick larvae do not descend vegetation to rehydrate like certain tick species (see Knülle and Rudolph 1982). After ascending, they remain on vegetation (Patrick and Hair 1975, Drew and Samuel 1985) and must employ alternative strategies to avoid desiccation and death when VPD is high. In 1984, the first larvae to ascend vegetation in the open plots were recovered 3–4 weeks after the initial appearance of larvae in closed cells at both sites. This delayed ascent was synchronous with the transition to cooler night air and abundant dew on vegetation (lower VPD) that would help rehydrate larvae permanently exposed after ascending vegetation, and might also account for why larvae appeared on vegetation earlier during the cooler September of 1984 as compared to 1983.

Timing of ascent by winter tick larvae varies annually with weather (Samuel and Welch 1991) and habitat in the same area (Patrick and Hair 1975, current study), and between ecosystems at the continental scale. For example, winter tick larvae experienced 4–8 month post-hatch delays before appearing on vegetation or hosts during October–November in warm climates of Texas, Oklahoma, and parts of coastal central California (Table 3). Ascent of vegetation at a south-facing site near Kamloops, British Columbia occurred as early as in central

Table 3. Timing of ascent of *Dermacentor albipictus* larvae.

Location	1 st Larvae on Vegetation	1 st Larvae on Host	Post-hatch Delay in Ascent
Edwards Plateau, Texas (1)		early Nov.	
San Antonio/Kerrville Texas (2)		Oct.	
eastern Oklahoma (3)			
- open meadow	Nov. 15		151 d
- forest	Nov. 15		133 d
central California (4)	Sept. 15	-Sept. 18 -Aug. 20–27	~ 4–8 mon
Kamloops, British Columbia (5)	Sept. 19 Oct. 3–6		~ 2 mon
central Alberta (6)	early Sept.		~ 2 wk
1985 (7)	Oct. 3		
1986 (7)	Sept. 30		
1987 (7)	Sept. 6		
1988 (7)	Sept. 11		
central Ontario (8)			
1983 opening	Sept. 6		
1983 forest	Sept. 13		
1984 opening	Aug. 28		17–24 d min
1984 forest	Sept. 18		25–32 d min

Numbers in parentheses refer to references: (1) Parish and Rude 1946; (2) Drummond 1967; (3) Patrick and Hair 1975; (4) Howell 1939; (5) Wilkinson 1967; (6) Drew and Samuel 1986; (7) Samuel and Welch 1991; (8) current study.

Alberta and central Ontario, but not until ~2 months post-hatch (Wilkinson 1967). In central Alberta and central Ontario, larvae were first reported on vegetation after a minimum post-hatch delay of 2–4 weeks (Table 3). Although the timing of transmission of winter tick larvae may seem to be an adaptation coincident with increased movement of moose during the mating season (Drew and Samuel 1985), the wide variation in the presence of larvae before ascending vegetation likely reflects a weather-induced evolutionary adaptation to reduce desiccation and mortality.

One disadvantage of delayed ascent could be a truncated transmission period that would occur more frequently in colder and more northern moose range; the opposite may explain more frequent epizootics in southern moose range. We collected limited

larvae following cold weather and substantial snowfall in 1983 and, like Drew and Samuel (1985), observed that larvae were much slower in response to movement and less effective in attaching to a flagging sheet at colder temperatures.

Summary

This study compared recruitment of winter tick larvae in 2 different habitats, a forest opening and a closed canopy, deciduous forest, by measuring survival of known adult female ticks and their productivity relative to weather. Recruitment varied annually both within and between habitats indicating that weather and microsite conditions influence recruitment of winter tick larvae. This influence was most important during the egg-laying and incubation periods in summer and

when larvae ascended vegetation in autumn. Open and warmer habitats are presumably the nidus for transmission of larvae to moose except in years of hot, dry weather in summer and autumn that increases egg and larval desiccation. The end of the diapause that occurs between hatching and ascent of vegetation appears synchronous with cooler, more humid conditions that would reduce desiccation of larvae both on the ground and questing on vegetation in late summer and autumn.

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