OVIPOSITIONAL DEVELOPMENT AND FECUNDITY OF *DERMACENTOR ALBIPICTUS* (ACARI:IXODIDAE) FROM MOOSE

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ABSTRACT: This study documents measures of productivity, under laboratory conditions, of winter ticks (*Dermacentor albipictus*) from Ontario moose (*Alces alces*). The data are used to understand variation in productivity of winter ticks in different parts of their range. The data will also be baseline data for estimating the number of larval ticks available to Ontario moose in the wild and to identify variables affecting availability of larval ticks to moose. The mean preoviposition period for engorged female winter ticks that had fed on captive moose was 13.5 and 8.8 days at 20°C and 24°C, respectively. The mean oviposition period for 40 females held at 24°C was 30.8 (15-36) days. Maximum mean daily production of eggs (655) occurred on day 5 of the oviposition period. We examined production and hatching of eggs in a variety of treatments that took into account possible influences of temperature, whether or not the ticks were from a moose with prior exposure to winter ticks, and whether or not the female ticks were disturbed daily during oviposition to collect eggs. Mean numbers of eggs laid/female varied between these treatment groups (6,263-8,255) and were about 50% higher than previously reported for *D. albipictus*. Times of development in the laboratory for *D. albipictus* from moose in Ontario were similar to values for winter ticks from other hosts and areas.

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Winter ticks (*Dermacentor albipictus*) have become recognized during the past 20 years as being harmful to moose (*Alces alces*). Large numbers of moose, heavily infested with winter ticks, were found dead in Alberta (Samuel and Barker 1979) and winter ticks were documented as the cause of premature loss of winter hair in moose (Glines and Samuel 1984, McLaughlin and Addison 1986, Samuel *et al.* 1986, Glines and Samuel 1989). Glines and Samuel (1989) reported weight loss, anemia and other blood physiological responses to ticks in captive moose. Addison *et al.* (1994) demonstrated reduced rates of growth in infested as compared to uninfested captive moose calves raised on high quality diets. Now that the significance of winter ticks to moose is more broadly accepted, we must understand the biology of the tick including its productivity if we are to predict when and where populations of moose may be adversely affected.

Dermacentor albipictus is distributed throughout southern Canada and much of the contiguous United States (Bishopp and Trembley 1945, Gregson 1956). Winter ticks vary greatly in appearance, size, and duration of the parasitic phase in different parts of their range (Cooley 1938, Ernst and Gladney 1975, Addison and McLaughlin 1988). Productivity of engorged female winter ticks held under laboratory conditions has been documented for ticks from Texas (Drummond *et al.* 1969) and Alberta (Drew and Samuel 1987) but not from east-

ern North America. Objectives of the present study are (1) to determine if production of eggs by winter ticks from moose in Ontario is similar to that from other areas, and (2) to establish baseline laboratory values against which productivity of winter ticks in the wild in Ontario can be compared.

METHODS

Moose were captured as calves, raised in captivity, and infested with larvae of *D. albipictus* of moose origin in 1980 (Addison *et al.* 1983, McLaughlin and Addison 1986). From March 28 to April 7, 1981, 392 engorged female ticks were collected after they detached from the captive moose. The engorged ticks were stored in damp sand at naturally fluctuating temperatures (-5°C to 22°C) for a maximum of 3 days before being washed, weighed, and placed individually in Petri dishes inside covered plexiglass terraria at 24°C (216 females) and 20°C (176 females). Ticks were examined daily for the presence of eggs. The preoviposition period was defined as the time from detachment of the female until the first egg was observed.

Eggs from 40 females held at 24°C were removed, weighed, counted and destroyed daily. The remaining females at both temperatures were left undisturbed once egg-laying had begun. Oviposition period was defined as the time between initial and final egg-laying. Following the oviposition period, egg masses from undisturbed females were weighed and returned to the incubators. This included about 1,000 eggs weighed and counted from each of 10 females at each temperature. The number of eggs produced by each female was estimated using the weight of the egg mass of the female and the calculated weight of an individual egg as determined from weighing the known number of approximately 10,000 eggs for that temperature. Egg masses were examined daily for the date of first larval hatch. Incubation period for an egg mass was defined as the time between appearance of the first egg and the first larva.

In November 1983, 3 captive 18-month-old moose were each infested with 21,000 larvae. Two of the moose had each been exposed to about 21,000 larvae during the previous year. The other moose had no prior exposure to ticks. Thirty engorged detached females were collected from the pens of each of the 3 moose on April 22-27, 1984 and were handled as described above for ticks in 1981. The engorged females in 1984 were incubated at 24°C and were left undisturbed until completion of egg-laying. Approximately 500 eggs were removed from each egg mass, weighed, and the eggs counted to determine the average egg weight from each egg mass. All eggs were returned to the incubators.

During all experiments, females and eggs within terraria were held over a saturated solution of potassium sulphate or potassium nitrate to maintain a high humidity (Winston and Bates 1960). Darkness was maintained except during examinations.

REI or "reproductive efficiency index" is the number of eggs produced per gram of female body weight (Drummond and Whetstone 1970). CEI is the "conversion efficiency index" and is the grams of eggs produced per gram of female body weight (Drummond and Whetstone 1970).

Engorged female ticks that died before laying eggs were removed from the experiment. A 2-tailed t-test was used to compare weights of the dead discarded females with weights of live females retained within each treatment group (Zar 1984). Analysis of variance was used to compare weight of engorged females, number of eggs, preoviposition period, incubation period, REI, and CEI between treatment groups (Morrison 1982). When statistical significance was found, differences were exam-

ined with the Newman-Keuls test (Zar 1984). Pearson correlation coefficients were calculated to evaluate the relationship between weight of female ticks and the number of eggs laid, the preoviposition period, and the oviposition period (Morrison 1982).

RESULTS

In 1981, 299 of 392 engorged female winter ticks survived throughout the oviposition period while in 1984, 74 of 90 females survived. Mean weights of engorged females within treatment groups were 0.81-0.88 g (Table 1). Ticks that died prematurely and did not lay eggs were similar in size to ticks retained within the same treatment group ($P>0.05$). Only data from surviving females are included in the results. Mean weights of engorged females were generally similar between treatment groups except between undisturbed females at 20°C and 24°C (Table 1).

The preoviposition period was about 5 days longer at 20°C ($\bar{x}=13.5\pm1.5$ days) than at 24°C ($\bar{x}=8.8\pm1.0$ days) and about 1 day longer for undisturbed females than for disturbed females at 24°C (Table 1). There was a weak negative correlation between the length of the preoviposition period and the weight of individual undisturbed females held at 20°C ($r=-0.237$, $P<0.05$) and 24°C ($r=-0.204$, $P<0.05$).

The mean oviposition period was 30.8 ± 4.9 days and varied from 15-36 days for individual ticks (Table 1). Egg laying at 24°C began rapidly and peaked on day 5 at a mean of 665/day. Most eggs had been laid within 21 days (Fig. 1). Sixty-six percent of all eggs produced were laid in the first 8 days of oviposition. There was a weak positive correlation between the number of eggs laid and the length of the oviposition period ($r=0.322$, $P<0.05$). The number of eggs laid was positively correlated with the initial weight of engorged female ticks in all 5 treatment groups (Table 1). The mean

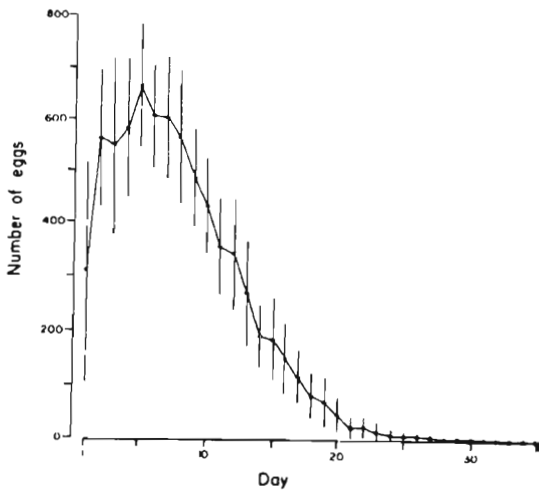

Fig. 1. Daily egg production of *Dermacentor albipictus* held at 24°C. Vertical lines indicate $\pm$ 1 standard deviation.

weight of eggs varied between 60.1 ± 4.1 µg and 71.4 ± 0.5µg among the 4 treatments held at 24°C.

The mean number of eggs laid/female varied from $6,263\pm1025$ to $8,255\pm1451$ among treatment groups. In most cases, more eggs were laid/female in 1984 than in 1981 (Table 1). REI and CEI values also were higher for ticks in the 1984 experiments than in the 1981 experiments. There were no consistently significant differences in eggs laid/female in relation to temperature (Table 1). However, females disturbed for daily collection of eggs laid more eggs and had higher REI values than undisturbed ticks from the same source held at both 20°C and 24°C (Table 1). The number of eggs produced/engorged female and the REI and CEI values for ticks from naive and previously exposed moose were similar (Table 1).

The incubation period was much shorter at 24°C ($\bar{x}=36.7\pm2.3$ days) than at 20°C ($\bar{x}=57.8\pm5.8$ days) and was similar between egg masses within each treatment group, particularly at the higher temperature (Table 1).

Table 1. Oviposition of *Dermacentor albipictus* from moose under laboratory conditions.

Factor	DISTURBANCE OF TICKS[1]			HOST[2]	
	Undisturbed	Undisturbed	Eggs removed daily as laid	Ticks off naive moose	Ticks off previously infested moose
Temperature	20°C	24°C	24°C	24°C	24°C
Number of females	160	99	40	25	49
$\bar{X}$(±SD) Weight of females (mg)	824 (142)[3,5]	882 (124)[6]	843 (112)[5,6]	873 (130)[5,6]	810 (148)[5]
$\bar{X}$(±SD) Eggs laid/female	6,365 (1666)[5]	6,263 (1530)[5]	7,297 (1025)[6]	8,255 (1451)[7]	7,512 (1660)[6,7]
Egg weight[4] (mg)	69.0 (0.4)[5]	71.4 (0.5)[5]	60.1 (4.1)[6]	62.7 (3.5)[7]	66.3 (4.3)[8]
Preoviposition period (days)±SD	13.5 (1.5)[5]	8.8 (1.0)[6]	7.6 (0.5)[7]	— —	— —
Oviposition period (days)±SD	— —	— —	30.8 (4.9)	— —	— —
Incubation period (days)±SD	57.8 (5.8)[5]	36.7 (2.3)[6]	— —	— —	— —
REI[9]: no. eggs/g female±SD	7,682 (1386)[5]	7,097 (1518)[6]	8,669 (608)[7]	9,443 (738)[8]	9,236 (895)[8]
CEI[10]: g eggs/g female±SD	0.530 (0.096)[5]	0.507 (0.108)[5]	0.520 (0.041)[5]	0.591 (0.039)[6]	0.609 (0.041)[8]
Correlation coefficients[11] of female weight vs eggs laid	0.747	0.565	0.885	0.919	0.913

[1] Disturbance of females for daily removal of eggs (1981)
[2] Previous exposure of moose to ticks (1984)
[3] Mean (standard deviation)
[4] Undisturbed (20°C and 24°C)-from a sample of 10,000 eggs from 10 females; disturbed (24°C) - average of all eggs laid; naive (24°C) - from a sample of 11,000 eggs from 25 females; previous (24°C) - from a sample of 23,000 eggs from 49 females
[5-8] Values in the same row followed by the same numerical superscript are not significantly different (Neuman-Keuls, $P>0.05$)
[9] REI = Reproductive efficiencey index
[10] CEI = Conversion efficiency index
[11] Pearson correlation coefficients all significant ($P<0.01$)

DISCUSSION

The parasitic stages of *D. albipictus* have shown great plasticity in their rates of development or times on their host (Addison and McLaughlin 1988). The parasitic phase varied from as short as 22-30 days on cattle in California (Howell 1939) and Texas (Drummond *et al.* 1969) to a minimum of 175 days from infestation to detachment from moose in Ontario (Addison and McLaughlin 1988). Similarly, winter tick has demonstrated great variation in morphology and size in different parts of its range (Cooley 1938, Ernst and Gladney 1975). Thus, it would not be surprising to also observe considerable variation in parameters of oviposition and fecundity during the free-living phase of winter tick. However, there were few differences in the ovipositional development and fecundity of winter ticks in Ontario as compared to other parts of North America.

The preoviposition period for engorged female winter ticks from Ontario held at 24°C (7-9 days) is similar to previously documented values for engorged female winter ticks from Alberta ($\bar{x}$ = 8.3 days at 25°C)(Drew and Samuel 1987). Both the Alberta and present Ontario preoviposition times are shorter than expected in comparison to the calculated values for winter ticks from Texas ($\bar{x}$ = 11.3 days at 27°C) (Drummond *et al.* 1969). The strong negative relationship between preoviposition period and temperature and weak negative relationship between preoviposition period and size of engorged females are known for other ixodids (Drummond and Whetstone 1970, Drummond *et al.* 1971, Davey *et al.* 1980a).

The mean number of eggs laid/female in the different treatment groups in this study (6,263 ± 1,530 to 8,255 ± 1,451) was 50% or more greater than for engorged female *D. albipictus* in previous laboratory studies (Bishopp and Wood 1913, Drummond *et al.* 1969, Glines 1983 from Drew and Samuel 1987, Drew and Samuel 1987). This is expected since engorged females in this study were much larger ($\bar{x}$> 0.8 g) than in previous studies ($\bar{x}$ = 0.39 to 0.69 g)(Drummond *et al.* 1969, Ernst and Gladney 1975, Addison and Smith 1981, Drew and Samuel 1987) and since larger female winter ticks are known to produce more eggs (Drummond *et al.* 1969, Addison and Smith 1981, Drew and Samuel 1987). The smaller female winter ticks and fewer eggs laid/female as reported for Ontario winter ticks by Addison and Smith (1981) are probably because the female ticks were not fully engorged when the moose they were on were killed in collisions with vehicles.

The large number of eggs laid in the first 8-10 days of egg laying in this study is similar to that reported for *D. albipictus* from cattle in Texas (Drummond *et al.* 1969) and is consistent with that of other ixodids (Drummond and Whetstone 1970, Davey *et al.* 1980a,b). However, the mean oviposition period of 30.8 ± 4.9 days for ticks held at 24°C in the present study was much longer than the mean oviposition period of 23.5 days calculated for *D. albipictus* held at 27°C (Drummond *et al.* 1969). Undoubtedly, the 3°C higher temperature in the experiments of Drummond *et al.* (1969) accelerated oviposition. However, the longer oviposition period in the present study may also in part be due to the much larger number of eggs being laid by *D. albipictus* in this study ($\bar{x}$=7,297) as compared to that reported by Drummond *et al.* (1969) ($\bar{x}$=3,864).

The incubation period in the present study (about 37-58 days) was similar to incubation periods for eggs of winter ticks from moose and other hosts (31-62 days) when eggs were held at 20-24°C (see Drew and Samuel 1987).

Higher REI values for disturbed than

for undisturbed females held at 24°C is consistent with a previous report of a positive correlation between disturbance and reproductive efficiency of female winter ticks (Drummond *et al.* 1969). However, we urge caution in interpreting this parameter until the effects of experimental methods on REI values are better understood. REI values from other studies of *D. albipictus* have been highly variable(5,729-9,200 eggs/g female) (see Drew and Samuel 1987).

Weight of eggs may differ between disturbed and undisturbed females because of differences in handling. Eggs from disturbed females were weighed and counted within 24 h of being laid whereas eggs from undisturbed females were not weighed until completion of the oviposition period. Perhaps eggs left over saturated solutions of potassium sulphate or potassium nitrate for longer periods of time absorbed moisture and increased in weight. Alternatively, dishes removed from the incubator daily for collection of eggs may have experienced lower humidity which may have reduced weights of eggs through desiccation.

Immunological competence and history of individual hosts may influence number of eggs laid by engorged female ixodids (McGowan *et al.* 1980, 1981; Chiera *et al.* 1985). However, there were no differences observed with the few moose used in the present comparative study (1 naive, 2 previously exposed).

In summary, the ovipositional development of *D. albipictus* from moose in Ontario studied under laboratory conditions is similar to ovipositional development of winter ticks from other hosts and areas. However, engorged female winter ticks from Ontario moose laid many more eggs/female than reported previously for winter ticks from other parts of North America. The Ontario ticks also appear to have laid eggs over a longer period of time. Both of these differences are likely attributable to the much larger size of winter ticks from moose in Ontario as compared to winter ticks from other areas.

While data presented in this paper do not seem immediately relevant to management of moose, they are very valuable in an indirect sense. We now have an initial understanding as to the maximum number of larval winter ticks that could be available to moose next autumn based on the numbers of engorged female winter ticks observed on moose in the spring. For example, an Ontario moose upon which 3,000 female winter ticks engorge in the spring could be the source of more than 20,000,000 larvae the next autumn if as many eggs are laid in the wild as in this study and if 100% of eggs hatch and larvae survive until autumn. Various habitat and weather conditions likely influence recruitment through to the larval stage in autumn. By comparing production of larvae in the wild with production of eggs under laboratory conditions, as in the present study, we will have a measure of the relative influence of natural variables on availability of winter tick to moose. Such studies are underway in Ontario.

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