WINTER TICKS ON MOOSE AND OTHER UNGULATES: FACTORS INFLUENCING THEIR POPULATION SIZE

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ABSTRACT: Research on northern populations of winter ticks (*Dermacentor albipictus*), particularly that relating to sources of variation in tick numbers, is reviewed. Mean numbers of ticks on moose (*Alces alces*) populations from 3 provinces were 32,527. Intrinsic sources of variation in size of tick populations included potential avoidance of sessile aggregations of larvae by moose in autumn, defensive grooming, and host death. Winter tick-induced premature loss of winter hair, which resulted from grooming, was prevalent and widespread throughout the southern range of moose in North America. Temporal progression and extent of hair-loss, and a proposed mechanism for that loss are reviewed. Extrinsic sources of variation in size of tick populations included effect of autumn weather on concentrations of tick larvae, and magpies on survival of shed adult female ticks. Reports of dead or debilitated moose with large numbers of ticks are numerous in Alberta and elsewhere. Whether winter ticks regulate moose numbers is not known, but moose are certainly the most severely affected host of winter ticks.

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The winter tick, *Dermacentor albipictus*, an acknowledged serious pest of moose (Anderson and Lankester 1974), is found throughout the southern range of moose in North America. It has also been reported in the Yukon Territory as far north as 62° (Samuel 1989), but not in Alaska (Zarnke *et al.* 1990). Where winter ticks occur on moose, they appear to cause a variety of problems including vigorous grooming (Samuel 1991), anemia and other physiologic effects (Glines and Samuel 1989), alopecia (Glines and Samuel 1984, 1989, McLaughlin and Addison 1986, Samuel *et al.* 1986, Welch *et al.* 1990), and reduced fat stores (McLaughlin and Addison 1986).

Numbers of winter ticks on moose from Alberta commonly exceed 50,000 (Samuel and Barker 1979, Welch *et al.* 1991) and epizootics of winter ticks have been associated with deaths of moose (Hatter 1950, Cowan 1951, Berg 1975, Samuel and Barker 1979, Addison and Smith 1981). Die-offs of moose in central Alberta have been associated with epizootics of winter ticks during at least 12 winters since 1930 (Webb 1959, Samuel and Barker 1979, Blyth and Hudson 1987); however, as Lankester (1987) has mentioned, "unequivocal evidence (of ticks being the cause of mortality) is lacking."

The objective of this paper is to review some results of the tick research program at the University of Alberta, 1978 - 1990. Data are presented on numbers of ticks on moose and other ungulates, prevalence and extent of tick-induced premature loss of winter hair on moose and other ungulates, and the effect of several intrinsic and extrinsic sources of variation on tick populations.

METHODS

Tick Numbers

Half-hides of 22, 19, 114, and 57 moose carcasses from northern British Columbia, near Rochester, Alberta, Elk Island National Park, Alberta, and Manitoba, respectively, were examined for winter ticks following techniques described by Welch and Samuel (1989). Briefly, numbers of winter ticks were estimated for each moose by dissolving 15% of 100 cm^2 quadrats of hide sampled at random in potassium hydroxide solution. Moose hides were taken from carcasses collected between late October and early April. Moose from British Columbia were killed by hunters in November and December, 1989. Most moose (17) from Rochester, Alberta were killed by hunters in late October, November, or early December of 1983 and 1987. Two other moose from Rochester were shot as encountered on 9 April 1981. Moose from Elk Island National Park were collected from December, 1977 to March, 1990. Most moose were collected as encountered with the provision that they were near a road and presented an easy killing shot. Sixteen of the 114 moose from the Park were found dead.

Prevalence and Progression of Hair-loss

The extent of tick-induced hair damage and alopecia over winter was assessed each spring between 15 April and 7 May from 1978 to 1990 by either aerial or ground surveys. Aerial surveys were conducted primarily in two study areas: a 180 km^2 area near Rochester, Alberta (54°22'N, 113°27'W) about 100 km north of Edmonton (1978 - 1990), and Elk Island National Park about 50 km east of Edmonton (1978 - 1990). Numbers of moose assessed totalled 292 and 300 at Rochester and Elk Island, respectively. Yearly sample sizes in each area exceeded 15 moose except at Elk Island in 1979 and 1981 (n = 0 and 5). For descriptions of these areas see Rolley and Keith (1980) and Drew and Samuel (1986), respectively. Additional aerial surveys were conducted at Long Lake Provincial Park (54°27'N, 114°45'W) (1981 only), located about 100 km north of Edmonton, and near the town of Swan Hills, Alberta (54° 43'N, 115°24'W) about 300 km northwest of Edmonton (1979 to 1981).

Surveys were conducted with a 206 Jet Ranger helicopter flying line transects at 0.2 or 0.4 km intervals at a speed of 120 km per hr and at an altitude of from 30 to 90 m above ground. Moose were kept in view until hair damage was assessed and drawn on a moose silhouette diagram. Often only one side of each moose could be drawn. In the laboratory the percentage of the silhouette of the torso covered by hair damage or loss was used as an index of alopecia. If both sides were drawn, the mean of both sides was used. Areas of damaged hair were measured using a digitizer (Bit pad two: Summagraphics Corporation, Fairfield, CT 06430).

A few additional ground observations were made near Jackson, Wyoming (1986), northeastern Utah (1987), Baxter State Park, central Maine (1986), Cypress Hills Provincial Park, southeastern Alberta (1988), and Riding Mountain National Park, west-central Manitoba (1988).

To determine the progression of hair damage/loss during winter-spring, aerial surveys were conducted at Rochester on: 7, 18, 30 March, and 14, 29 April 1980 (with sample sizes of 21, 21, 21, 20, and 22 moose, respectively); 4 February, 3 March, 2 and 23 April 1981 (n = 18, 21, 19, and 20, respectively); 25 March and 27 April 1982 (n = 22 and 17); and 4 February, 1 March, 6 and 25 April 1983 (21, 25, 20, and 16, respectively). Over 300 observations were made.

Aerial and ground surveys were conducted at Elk Island National Park on: 8 days between 16 January and 29 April 1980 (sample sizes all over 20); weekly from 10 January to 1 May 1986 (sample sizes from 4 to 18); weekly from 5 February to 22 April 1988 (n = 5 to 24); and weekly from 10 January to 21 April 1989 (n = 4 to 35). Park roads were driven during ground surveys. About 700 observations were made.

These indexes of tick-induced damage to the winter hair of moose are more conservative measures of alopecia than total volume of lost hair (McLaughlin and Addison 1986). Based on results for captive moose experimentally infested with winter ticks, they underestimate the extent of hair damage depending on the date of the survey in any year because hair loss progresses through April (Welch *et al.*, 1990) and surveys were run as early as 15 April.

Moose Aversion to Tick Larvae

In October and November 1986, and January 1987, a preliminary experiment was conducted to determine whether moose detected and avoided sessile aggregations of winter tick larvae. On 6 occasions between 29 October and 9 January, a captive 2-year-old female moose, deprived of her usual pelleted food ration for 12 hr, was offered 2 identical pails of pelleted food side-by-side (1 m apart), 1 with approximately 10 large aggregations of larvae (*i.e.*, estimated total of several thousand), 1 without. In 1 of the 6 trials, very few food pellets were placed in each pail. The cow had been infested experimentally with winter ticks in 1984 and 1985. Behavior, feeding frequency and length at each pail were recorded. A 'feeding' bout consisted of the moose putting her head in the pail.

Effect of Weather on Aggregations of Tick Larvae

Many larvae were placed in the center of a 10 x 10m^2 outdoor naturally-vegetated plot of weeds on the University of Alberta campus on 20 September 1985. Vegetation in the plot was checked daily for aggregations of larvae for 2 months. Daily weather data including cm snow, mean and maximum wind (km/hr), and maximum, minimum, and mean temperatures were compiled from monthly meteorological summaries of Environment Canada from the nearby Edmonton Municipal Airport.

On 25 July 1986, 31 uncapped vials with unhatched eggs from individual adult female ticks were placed in the litter at the foot of each of 6 wooden fence posts in a grassy field near Edmonton and at the base of 26 small aspen trees (diameter at base 2 - 3 cm) at the edge of the same grassy field. The trees were cut to a height of either 50, 100, or 150 cm and were surrounded by circular screenwire cages 30 cm in diameter and 40 cm high (modeled after Semtner *et al.* 1973). The vials were placed on their side to prevent filling with moisture. Vials and vegetation nearby were checked for aggregations of larvae every 2 to 5 days from 12 August until 17 November. Daily weather data were compiled from Environment Canada data from the nearby Edmonton International Airport.

On 7 and 24 April 1987 and 1988, times corresponding with the peak and end of tick drop-off from moose, respectively, individual shed engorged adult females in separate vials were placed at the base of the same 26 small aspen trees as in 1986. They were checked weekly for aggregations of larvae from 10 August until 27 and 6 December 1987 and 1988, respectively. Survival of larvae was determined by blowing on aggregations and recording questing behavior until 1 November when small numbers were collected from several very large aggregations, taken to the laboratory, and observed.

Feeding or Caching Ticks by Magpies

Twenty-four captive black-billed magpies (*Pica pica*) were offered, as a food source, the engorged adult female stage of the winter tick and/or shed winter hair of moose in addition to their usual food, dogfood pellets. The two-part experiment (hereafter called Trials 1 and 2) was conducted in early May 1987, utilizing 12 adult (4 males, 8 females) and 12 juvenile (3 males, 9 females) black-billed magpies. All of the magpies used in the 2 experiments were captured within the city limits of Edmonton where it is assumed they had no or minimal previous contact with winter ticks. Because engorged female winter ticks are only found in spring, the 12 juvenile birds did not have previous contact with ticks, having been captured shortly after fledging. Birds were held in captivity from 6 to 18 mo prior to the study.

Holding facilities were an outdoor wire-mesh enclosure 9.8 x 3.6 x 1.9 m (flight cage) attached at one of the narrow ends to a 1.8 x 3.6 x 2.3 m observation hut. A window of one-way glass allowed unobtrusive observation of birds in the flight cage. The ground surface in the cage was mostly exposed small rocks and soil, with some grass and weeds.

Magpies were previously housed in 2 of these cages (12 per cage) and fed pelleted dog food and water *ad libitum*. Dog food was removed 18 hr before the initiation of each trial. Birds were not unduly stressed by this length of food deprivation; they commonly roost for approximately 12 hr in Edmonton at temperatures as low as -30°C (Reebs, 1986).

The 24 birds were captured and held in the observation room immediately prior to each trial. Each of 4 plastic containers (19 x 28 x 11 cm) was placed on the ground 30 cm apart at the far end of the flight cage. Each contained one of the following: pelleted dog food (number of pellets not determined), shed winter hair from moose, shed moose hair and 15 live engorged adult female *D. albipictus*, 15 live engorged adult female *D. albipictus*, and grit.

Birds were chosen arbitrarily and released individually for 10 min into the cage. Every bird flew to the plastic containers immediately. Movements between containers, number and duration of feeding sessions, and ingestion and caching of food items were recorded in order. A feeding session initiated (and concluded) when a bird perched on (and off) a food container. A tick or dogfood pellet was assumed ingested when a magpie took the item into the beak and swallowed. In many cases, several dogfood pellets were taken at one time and eaten too quickly to be counted accurately; thus, numbers of dog food pellets eaten are conservative minimal estimates. When a tick was not swallowed it was readily seen in the partially opened beak or was assumed to be present in the oral cavity.

After each 10 min observation period, birds were removed from the cage, food was replenished in the containers, and cached ticks were sought. At the end of Trial 1, birds had access to all food items *ad libitum* for 24 hr. Food was then removed 18 hr before the beginning of Trial 2. In Trial 2, the same 24 birds were used and the same format followed as described above except that containers were rearranged.

RESULTS

Tick Numbers

The mean number and ticks per cm² skin surface of winter ticks on 212 moose from 3 western provinces were 32,527 and 1.43, respectively (Table 1). The maximum number of ticks recovered from one moose was 149,916; 18% of moose had infestations numbering over 50,000, 6% had over 80,000 ticks. As expected, frequency distributions of tick numbers were skewed (Fig. 1). Although there was much variation in numbers between moose, mean total numbers and ticks per cm² skin surface exceeded 25,250 and 1.1, respectively, for all moose populations sampled (Table 1).

At Elk Island National Park mean tick numbers varied considerably between years (Fig. 2). Numbers were highest in the winters of 1981 - 1982 and 1987 - 1988 when most and a few moose died, respectively. During those winters 8 of 19 and 3 of 17 moose hides digested came from moose found dead. Lowest numbers and densities occurred in 1983 - 1984, 2 years after a major tick-related die-off of moose in the Park.

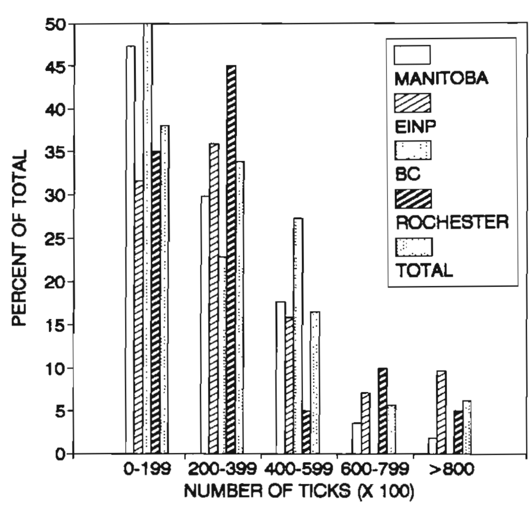

Fig. 1. Frequency distributions of the numbers of winter ticks on moose from 4 areas of Western Canada.

Table 1. Estimates of total numbers and densities of winter ticks on moose of western Canada with percentages of moose with high numbers of ticks.

Location	n	Total mean number (std dev)	Density (ticks/cm^2)	% moose with numbers > 50000	% moose with numbers > 80000	Range Max.	Range Min.
Northern BC*	22	25258 (17606)	1.16	14	0	59985	3459
Manitoba	57	26446 (20330)	1.17	18	2	97704	2867
E.I.N.P.*	114	37070 (29191)	1.66	20	10	149916	5042
Rochester*	19	31933 (21036)	1.11	15	5	84276	2774
Totals	212	32527 (25840)	1.43	18.4	6.1		

* BC = British Columbia; E.I.N.P. = Elk Island National Park, Alberta; Rochester, Alberta.

Winter ticks were found on other hosts from Elk Island National Park including: elk (*Cervus elaphus*) (x = 3406, n = 43), white-tailed deer (1465, n = 10), and plains and wood bison (*Bison bison bison* and *B.b. athabascae*, respectively) (175, n = 8). Elk from Jackson, Wyoming (Samuel *et al.* 1991), and woodland caribou (*Rangifer tarandus caribou*) from western Alberta (Welch *et al.* 1990a) were also infested (x = 3960, n = 9; x = 48, n = 3, respectively).

Prevalence and Progression of Hair-loss

A total of 724 moose from 9 areas in 2 provinces and 3 states were observed for tick-induced premature damage or loss of winter hair at winter's end between 1978 and 1990 (Table 2). Most (89%) had some degree of hair damage/loss attributable to infestation with *D. albipictus*.

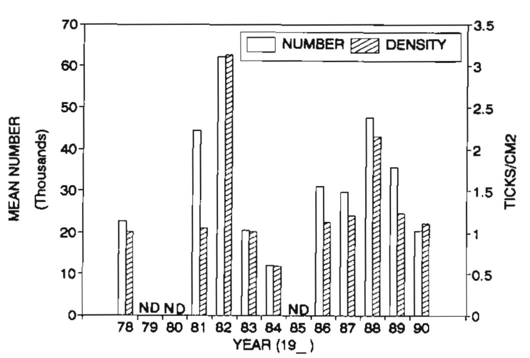

Fig. 2. Estimates of total numbers and densities of winter ticks on moose of Elk Island National Park, Alberta, 1978 - 1990.

Tick-induced hair damage or loss was extensive in the moose population at Rochester, Alberta, and much less so at Elk Island National Park (Fig. 3). At the end of 8 of 13 winters at Rochester (none at Elk Island Park), the mean amount of hair damaged or lost prematurely was over 40% of the lateral torso.

Generally, hair damage was first noticed in February at Rochester and March at Elk Island Park (Fig. 4). By mid-April the average amount of hair damage on moose from Rochester was 49, 45, 66, and 79% for the years 1980 - 1983, respectively, while at Elk Island Park end of winter percentages for the years 1980, 1986, 1988, and 1989 were 31, 22, 49, and 21, respectively.

Moose Aversion to Tick Larvae

The cow moose used in the tick aversion experiment avoided pelleted food artificially

Table 2. A summary of the prevalence of tick-induced hair damage or loss on moose observed between 1978 and 1990 in various states and provinces.

Location	*n*	Number (%) moose with hair-loss
Alberta		
Rochester	292	285 (98)
Elk Is. National Pk.	300	265 (88)
Long Lake Prov. Park	20	20 (100)
Swan Hills	71	48 (68)
Cypress Hills Prov. Pk.	5	3 (60)
Manitoba		
Riding Mtn. National Pk.	4	4 (100)
Wyoming		
Jackson	22	7 (32)
Utah		
Ogdon	3	3 (100)
Maine		
Baxter State Park	7	7 (100)
Totals	724	642 (89)

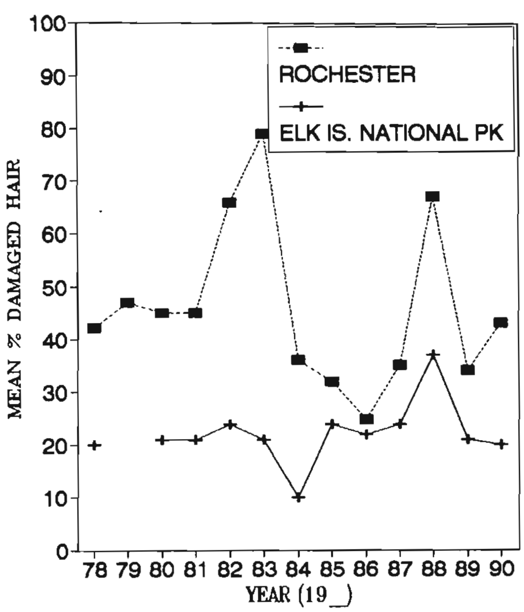

Fig. 3. Mean percent winter tick-induced damage and alopecia to the haircoats of moose from Elk Island National Park and Rochester, Alberta, 1978 - 1990.

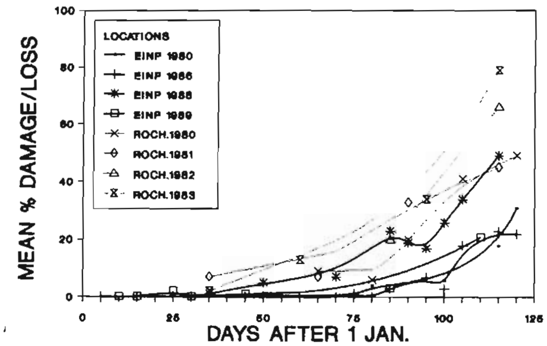

Fig. 4. Progression of winter tick-induced damage and alopecia to the haircoats of moose from Elk Island National Park and Rochester, Alberta for 4 years between 1980 and 1989.

infested with tick larvae in 5 of the 6 trials (Table 3). Only in Trial 3 (where few food pellets were placed in either pail) did she feed extensively in the infested pail. In that trial, the cow sequentially fed 9 times from the uninfested pail, once (2 sec) from the infested pail, once from the now empty uninfested pail (6 sec), then 10 times from the infested pail. In all 6 trials she immediately approached the pails when introduced into the test paddock, moved her head to within 15 cm of each pail, and began feeding from the uninfested pail. During Trials 4 to 6, the cow appeared very excited and would pace nervously after putting her head near the infested pail. Near the end of Trials 2 and 3, the cow groomed ticks as described by Samuel (1991).

Effect of Weather on Aggregations of Tick Larvae

Aggregations of tick larvae began appearing on tips and high parts of the weed-type vegetation in the campus enclosure on 3 October 1985 (Fig. 5). Aggregations began appearing on tips of small limbs or at the top of the aspen trees on 30, 6, and 11 September 1986 to 1988, respectively (Fig. 6). A few larvae were found on the top rim of the screenwire cages and at the tips of short grasses next to the aspen trees. In all 4 years, number of aggregations increased steadily for several days until mid-to-late October, when major

Table 3. Summary of results of exposure of captive cow moose to tick-infested and uninfested pelleted food.

Trial Number	Date	Trial length (min)	Number of feeding bouts Infested	Number of feeding bouts Uninfested	Mean length (sec) each bout Infested	Mean length (sec) each bout Uninfested
1	29 Oct	67	0	3	0	24.7
2	30 Oct	79	3	22	3.7	19.3
3*	31 Oct	24	11	10	15.2	17.2
4	26 Nov	93	0	11	0	12.7
5	27 Nov	19	0	7	0	13
6	9 Jan	135	0	20	0	11.9
	Total	417	14	73	12.5	15.6

* Few food pellets were placed in each pail.

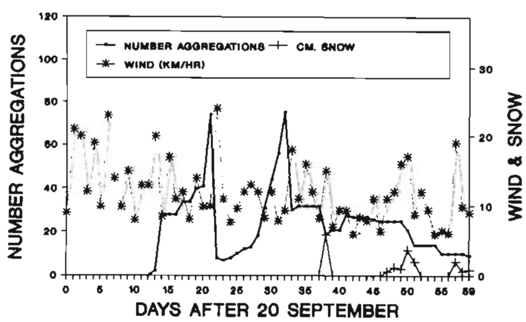

Fig. 5. Number of aggregations of winter tick larvae on vegetation in an enclosure plot, and amount of snow and wind, on campus, University of Alberta, 1985.

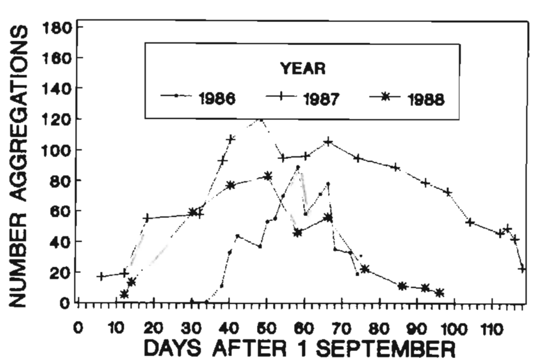

Fig. 6. Number of aggregations of winter tick larvae on vegetation in a small young stand of aspen, Ellerslie Research Station, University of Alberta, 1986 to 1988.

declines were observed (Figs. 5 and 6). Wind and snow were the major factors involved in the losses. The 2 major losses in 1985 (74 to 8 and 75 to 30 aggregations on 12 and 23 October, respectively) were attributable to strong winds (mean of 24 and 18 km/hr, respectively, with maximum > 33 km/hr) (Fig. 5); later, the first snowfall of the autumn (5.8 cm on 28 October) buried 12 aggregations of larvae (Fig. 5). Wind, snowfall and the first cold temperatures (mean below 0°C) likely accounted for losses in numbers of aggregations after day 50 (= 9 November).

In 1986, the first major loss occurred between 27 and 30 October when the number of aggregations decreased from 89 to 58 (Fig. 7). Snow (1.6 cm) fell during that time and mean and maximum winds on 30 October were 22 and 44 km/hr, respectively. The second loss occurred on 7 November when 43 of 78 aggregations of larvae disappeared. Mean and maximum windspeeds on that day were 30 and 43 km/hr, respectively; snowfall on that day and the evening of the preceeding day totalled 9.2 cm. (Maximum winds on 6 November were 46 km/hr.) Wind and the first severe cold (mean temperatures below -17°C for 6 consecutive days) likely accounted for steady losses in numbers of aggregations after day 38 (= 7 November). On 13 Novem-

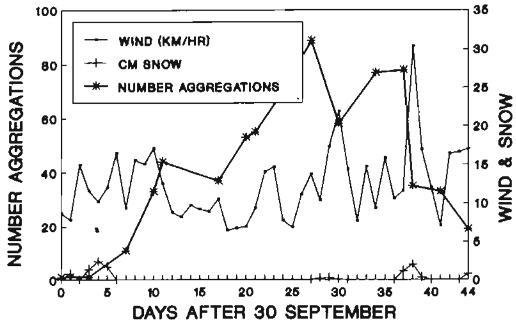

Fig. 7. Number of aggregations of winter tick larvae on vegetation in a small young stand of aspen, and amount of snow and wind, Ellerslie Research Station, University of Alberta, 1986.

ber, only 1% of the larvae in 19 aggregations were alive.

Less detailed records were kept during 1987 and 1988 (Fig. 6), but during the warm autumn of 1987 the first losses in mid-October occurred during the first period of cold windy weather (October 23). Over 95% of larvae were alive on 7 December 1987, compared to 35% survival on that date in 1988 (Fig. 8).

Feeding/Caching Ticks by Magpies

The only clear results relating to food preference were that magpies ate or cached a lot of ticks and dogfood pellets, and did not eat moose hair (Table 4). Magpies feeding in containers with moose hair and ticks ignored

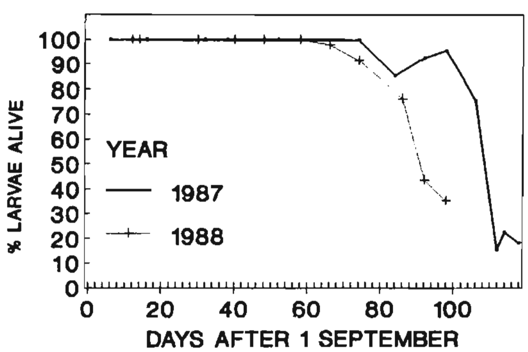

Fig. 8. Percent living winter tick larvae on vegetation in a small young stand of aspen, Ellerslie Research Station, University of Alberta 1987 and 1988.

or removed much of the hair with their bill, then took ticks. There were few differences between Trials in the number and length of feeding sessions, containers visited first, or food item eaten first (Paired Student's t-test, $P > 0.05$). In 392 feeding sessions and 480 min of observation, magpies visited containers with ticks and dog food pellets 196 and 106 times, respectively, and the mean length of visits to containers with ticks and dogfood pellets was 8.7 and 12 sec, respectively.

Magpies cached more ticks (169) than they ate (74) (Gadj. = 5.59; df = 1; P = 0.018), and ate and cached more ticks in Trial 2 than in Trial 1 (G_{adj} = 100; df = 1; P < 0.0001) (Table 4). They ate and cached 88 and 81 dog food pellets, respectively. The mean number of ticks and pellets taken at each visit to a container was 1.2 and 1.6, respectively. Five birds did not eat or cache ticks in either trial; 1 bird did not eat or cache dog food pellets.

The maximum number of ticks eaten and cached by a bird in both trials (= 20 min total observation time) was 11 and 24, respectively (both by the same bird). The maximum number of dog food pellets eaten or cached by a bird in both trials was 7 and 7, respectively.

Ticks were cached in the only available litter associated with the little grassy vegetation in the enclosures. A total of 95 *D. albipictus* cached by magpies were recovered from 19 caches (x = 5; range 1 - 11). All ticks were alive; the exoskeleton of 1 had been damaged slightly.

DISCUSSION

The few sources of variation in tick populations for which new data are presented here include premature loss of winter hair (the assumption being that as hair is lost to grooming by moose, so too are ticks), moose avoidance of sessile aggregations of larvae, the effect of autumn weather on concentrations of tick larvae, and the effect of magpies on survival of shed adult female ticks in late winter-early spring. Winter ticks probably

Table 4. Numbers of feeding sessions, winter ticks, and dogfood pellets eaten or cached by 24 captive black-billed magpies.

		Trial Number 1		Trial Number 2		Total
Number of visits to containers		189		203		392
Number (%) involving:	ticks[a]	82	(43)	114	(56)	196 (50)
	dogfood	54	(29)	52	(26)	106 (27)
	hair/grit	53	(28)	37	(18)	90 (23)
Number feeding sessions		88		136		224
Number involving:	ticks	48		94		142
	dogfood	40		42		82
	other items	0		0		0
Number of ticks available		720		720		1440
Number (%) eaten		23	(3)	51	(7)	74 (5)
Number (%) cached		29	(4)	140	(19)	169 (12)
Dogfood pellets						
Number eaten		46		42		88
Number cached		13		68		81

[a] Includes containers with *D. albipictus* only and *D. albipictus* and moose hair.

affect moose in the same way other arthropod parasites affect other hosts (Sutherst, 1987); *i.e.*, by 1) irritating moose so that they groom, thus disrupting feeding and resting behavior, 2) removing blood, and 3) producing toxins that alter metabolism. There are no data for winter ticks relating to the last point but assumed problems relating to the first two points that have been mentioned in the literature include:

a. high numbers of ticks (Samuel and Barker 1979), which lead to;
b. stimulation of the immune respoonse by feeding larvae, nymphs or adult ticks, thus initiating the first line of defense against ectoparasites, grooming (Samuel 1991). Grooming results in
c. premature loss of hair in late winter (McLaughlin and Addison 1986, Samuel *et al.* 1986, Glines and Samuel 1989) and the bioenergetic consequences, including reduced fat stores, of that alopecia (McLaughlin and Addison 1986, Welch *et al.* 1990);
d. removal of many ticks by grooming thus interrupting the blood-feeding process and, as a consequence, decreasing the reproductive rate of the tick (Glines and Samuel 1989, Barker *et al.* 1990), and;
e. depressed levels of many blood components including RBC's, hemoglobin, hematocrit and serum albumin by feeding ticks (Glines and Samuel 1989).

Regarding numbers of ticks on individual moose, Samuel and Barker (1979) provide preliminary information indicating that numbers occasionally exceed 100,000. In the present study we used a more accurate technique for determining numbers of ticks on moose (Welch and Samuel 1989) than did Samuel and Barker (1979) and found that 13 of the 212 moose half-hides digested for ticks had over 80,000 ticks. The very high number of ticks we report here from moose will directly affect the first two of the above three points; in particular, one can easily visualize the detrimental affect that feeding ticks have on blood components (Glines and Samuel 1989). In addition, populations of winter ticks on experimentally-infested moose produce more and larger engorged females than do equivalent infestation on elk, mule deer (*Odocoileus hemionus*), or white-tailed deer (Welch *et al.* 1991).

Captive moose uninfested and experimentally infested with winter ticks spend < 0.5% and > 5.5% of their time, respectively, grooming ticks between February and April (Samuel 1991). Tick-infested moose also spend less time lying down than do control moose (Samuel 1991).

Winter ticks cause far more alopecia on moose than on elk or deer (Welch *et al.* 1991), but the significance of this for moose is unknown. As shown here, most hair-loss occurs in March and April, when temperatures are seldom severely cold. Hypothermia does occur (Glines and Samuel 1989) and might be common during very cold winters, but during the many recent mild winters experienced across southern moose range in North America, tick-induced alopecia may impose only nominal thermoregulatory costs on moose (Welch *et al.* 1990). We suggest that expenditure of energy to grooming, especially for pregnant cows, but also for undernourished moose emerging from winter, is a more important cost to moose than thermoregulatory costs.

Aversion of Moose to Aggregations of Larvae

The larva is an important life stage of the winter tick. In central Alberta larvae climb vegetation in autumn and aggregate on the tips of vegetation (Drew and Samuel 1985, and this study). It is assumed that moose become infested passively as they touch tick-infested vegetation during usual autumn activities. Drew and Samuel (1985) suggest that transmission of larvae to moose is probably facilitated by synchrony of the peak numbers of larvae on vegetation in late September - early October with increased activity during the moose breeding season. During certain autumns, many large aggregations of larvae are common, particularly at sites where moose died the previous late winter and spring (Drew and Samuel 1985; Samuel unpub.). The densities and sizes of aggregations at carcass sites and used in the present experiment were similar. Preliminary data presented here suggest that moose are able to detect large numbers of winter tick larvae and avoid them. If this regulating mechanism is operating in nature, decreased transmission of *D. albipictus* to moose is possible.

The first report of this unique form of population regulation for ticks was provided by Sutherst *et al.* (1986) who found that cattle detect and avoid high densities of the tick *Boophilus microplus*.

Effect of Weather on Aggregations of Larvae

Wind, snow, and temperature, are important in the autumn transmission of winter tick larvae from vegetation to vertebrate hosts in central Alberta. Aggregations of larvae are affected by high winds that scatter, snow that covers, and, in November, low temperatures that inactivate. Drew and Samuel (1985) found that larvae of *D. albipictus*, once they ascend vegetation and form aggregations on the tips of vegetation, remain there until they either transfer to a host, are blown off, or die. Also, they observed that all larvae are active and questing at temperatures above 10°C, but at 0°C it takes 2^{+}min of exposure to human skin for them to become active. Thus, although larvae can survive in aggregations until well past November in central Alberta, we can assume that transmission essentially is complete when either temperatures drop below 0°C or aggregations are lost due to dispersal by wind or burial under snow; *i.e.*, by late October. Larvae present on vegetation in November, December and later probably are either too inactive to be transferred easily to a host or are dead.

Magpies Feeding/Caching Ticks

In Western Canada, black-billed magpies are known to sit on, and apparently ingest ticks (*Dermacentor albipictus* and/or

Dermacentor andersoni) from, wild ruminants such as Rocky Mountain bighorn sheep (*Ovis c. canadensis*) (Green 1949, Stelfox 1968), Rocky Mountain mule deer (*Odocoileus h. hemionus*) (deBoon 1986), and moose (deBoon, 1986; pers. observ.).

In Alberta, where virtually every moose is infested with winter ticks, magpies are presented with an abundant, albeit temporary, food source in March and April when ticks are engorging on (then dropping from) moose. During this time it is common to see magpies land on moose or at moose bedding sites in the snow, seemingly foraging (= pecking) for ticks. Such behavior has been reported for ravens, *Corvus corax*, and gray jays, *Perisoreus canadensis*, in Ontario (Addison *et al.* 1989). Of the several reports suggesting that magpies eat ticks of the genus *Dermacentor*, only Green (1949) and Petrischeva and Zhmayeva (1949, in Wilkinson 1969) killed birds and recovered ticks. Green (1949) watched magpies apparently feeding on ticks on bighorn sheep, shot 6 of the birds, and recovered from 3 to 16 engorged female *Dermacentor* sp. from their stomachs. According to Wilkinson (1969), Petrischeva and Zhmayeva (1949) identified 160 ticks of 8 genera in the stomachs of 12 magpies.

Henny *et al.* (1985) report that cattle hair comprises 12% of the gizzard contents of magpies apparently killed by an organophosphate insecticide used to kill warbles on cattle. They suggest that the ingestion of cattle hair by magpies "may have first developed from the symbiotic relationship.between magpies and wild ungulates, elk, buffalo, and mountain sheep. Thus the cow hair may be performing the function (unknown at this time) originally provided by wild ungulate hair." In the artificial setting of the present experiment, magpies ate or cached ticks, not hair. It is our contention that the main players in the symbiotic relationship mentioned are magpies and ticks, not magpies and ruminant hair.

The fact that magpies in this experiment, with no prior direct experience with ticks, both ate and cached blood-engorged winter ticks has important or potentially important consequences for moose, magpies and ticks. Potentially, it is advantageous for moose to let magpies remove ticks from them whether the ticks are ingested or cached. In Alberta it is common to see magpies sitting on the backs (or clinging to the sides) of moose in March and April apparently eating ticks (pers. observ.). Up to 3 magpies have been observed on a moose. During one such observation a magpie appeared to be removing ticks from the moose and caching them in foot prints made by the moose in the snow. Moose have not been observed responding negatively to the presence of magpies on their back or neck, suggesting that this association is an example of protocooperation (Isenhart and De Sante 1985).

Magpies hoard or cache food as a future food source, but if they do not soon utilize their ground caches (*i.e.*, before early June when ticks oviposit [Drew and Samuel 1986]), then caching could potentially result in increased survival and dispersal of engorged female ticks, and larger tick populations to harass moose in subsequent years. In the present study, ticks cached in the enclosure were alive, uninjured and buried in litter in areas that subjectively appeared to be suitable (*i.e.*, moist, protected areas) for survival of the engorged female tick (hence, her progeny). If they were able to relocate even a short distance, they might avoid being eaten by magpies later. Unfortunately, the number of cached ticks recovered and eaten by magpies in nature is unknown. However, the availability of natural food for magpies of central Alberta has been shown to be in short supply in March-April, the time of nest building and clutch initiation (Hochachka and Boag 1987). Ticks, including those cached, may be an important locally abundant food source for magpies at this time.

Perhaps complicating this picture is the fact that magpies are territorial and cache their food in their territories (Clarkson *et al.* 1986). A magpie would not be expected to follow a moose far outside its territory, especially during the breeding season, to collect ticks. When a tick-infested moose moves through the territory of a magpie, that bird might be expected to collect and cache as many ticks as it can.

While it is clear that winter ticks may present an important, locally abundant food source for magpies in March and April, it is unclear if magpie predation counteracts or enhances population growth of ticks and if predation has, as a consequence, an indirect positive or negative impact on moose populations. Future research should investigate this potentially important relationship. Magpies would seem not to lose in this interaction. If magpies disseminate ticks through caching, and larger tick populations result, ticks may present a more abundant food source in subsequent years. Alternatively, moose die-offs could occur resulting in moose carcasses for magpies to scavenge.

It is not known how long winter ticks, moose and magpies have coexisted. *Dermacentor albipictus* is widespread in North America and is especially abundant in southern Canada and the northern United States (Anderson and Lankester 1974). The tick was originally described from moose from Nova Scotia, Canada in 1869 (Hayes and Packard 1869), at which time its pest-like qualities for moose were also described (Hardy 1869, in Anderson and Lankester 1974). Anderson and Lankester (1974) suggest that moose are a newly acquired host for winter ticks with deer (*Odocoileus* spp.) possibly serving as the original host.

In Western Canada, tick problems on moose likely became prevalent in the early 1900's when agricultural and forestry practices resulted in vegetative succession conducive to white-tailed deer. As deer numbers increased, transfer of winter ticks to moose likely occurred. Magpies, an ecotonal species that in Alberta rely heavily on agriculturally produced carrion (Kalmbach 1927), probably became numerous at the same time. As numbers of ticks became numerous on moose, magpies likely became more predatory on this extensive, transitory food source.

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