GROOMING AND RUBBING BEHAVIOR BY MOOSE EXPERIMENTALLY INFESTED WITH WINTER TICKS (*DERMACENTOR ALBIPICTUS*)

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ABSTRACT: Rates of grooming, rubbing, and shaking were observed of 12 moose (*Alces alces*) infested with 4 levels of winter ticks (*Dermacentor albipictus*) and 5 uninfested control animals. Modes of grooming varied among moose and occurred with the tongue, hind feet, head, ears, antlers, teeth, and neck. Only moose with ticks used teeth and ears to groom. Uninfested moose and moose prior to being infested groomed and rubbed little. Grooming was greater immediately following than before infestation, and initial grooming and rubbing were predominant at the sites of infestation. Grooming declined in mid-winter months when nymphs develop slowly and increased in late winter and early spring when nymphs and adults actively feed; rubbing only increased in late winter and early spring. Cumulative grooming-rubbing was positively correlated with level of tick infestation and hair loss, and negatively correlated with end body weight of female calves only. Intense individual bouts of grooming and rubbing during April lasted 13–141 min. Over the entire study, cumulative grooming-rubbing in daylight hours for moose with 21,000–42,000 larvae equaled 6–28 d (μ = 12.7), and from February to April moose with 42,000 ticks groomed and rubbed on average ≥5.0–7.5 min/h. The removal of ticks was high (77–96%) indicating that grooming and rubbing are positive behavioral responses with respect to reducing the impact of winter ticks.

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Grooming and rubbing behavior by captive moose (*Alces alces*) infested with winter ticks (*Dermacentor albipictus*) were previously described by individual actions and temporal changes in behavior during mid-late winter (Samuel 1991). Welch et al. (1991) further documented grooming behavior throughout the infestation period and found that winter ticks stimulated grooming and rubbing in moose and that these behaviors varied with tick phenology. Observations of free-ranging moose in Elk Island National Park, Alberta documented that calves groom more than adult moose, limited grooming occurs from October to February, extensive grooming occurs in March and April, and a positive correlation exists between grooming activity and hair loss (Mooring and Samuel 1998a, 1999).

By controlling the level of infestation of winter ticks on captive moose, our research augments previous research by testing 6 null hypotheses: 1) grooming and rubbing is similar for moose infested and not infested with winter ticks, 2) grooming and rubbing is similar regardless of the level of infestation, 3) grooming and rubbing is similar before and after infestation, 4) grooming and rubbing is similar regardless of the site of infestation, 5) grooming and rubbing is consistent throughout the phenology of winter ticks, and 6) hair loss is independent of the amount of grooming and rubbing. Our study further evaluated the relationship between cumulative grooming and rubbing activity and body mass of moose late in the infestation period.

METHODS

Calf moose used in this study were raised in captivity in 1980 (n = 2), 1981 (n = 4), and 1982 (n = 18) in Algonquin Provincial Park, Ontario (45° 33'N, 78° 35'W) as described by Addison et al. (1983). Each pen (29.6 × 16.5 m) had an observation booth positioned 3 m high at the back of and straddling the midline of each pair of pens. Winter tick (tick hereafter) larvae were collected annually during September and October 1980–1982 by dragging flannel sheets over vegetation, then removing and counting the attached larvae.

In Year 1 (1980 – 2 calves), one calf was infested with 1000 larvae and the other with 8000 larvae on one side only on 11 November. In Year 2 (1981 – 4 calves), 2 calves were infested on 25 and 26 September, one with 20,000 larvae applied to the right side of the body, the other with 22,000–23,000 larvae applied to the dorsal and upper lateral surfaces; 2 calves were maintained as controls. In Year 3 (1982 – 18 calves), ticks were applied on the dorsal and upper lateral body surfaces from 17 September – 12 October. The initial half was applied by 24 September – 2 October; 30 September was designated as the date of infestation for all animals. Three treatment groups were established: 1) 4 calves received 21,000 larvae, 2) 4 calves received 42,000 larvae, and 3) 4 calves served as controls. The remaining 6 calves (reference animals) served to document growth and developmental stages of ticks in the captive herd (Addison and McLaughlin 1988).

During application of larvae in 1981 and 1982, calves were tethered on a short lead for 30 min to prevent them from grooming and allow larvae to reach the skin. In 1982–1983, a 1.6 % liquid solution of Sendran [(2-propan-2-yloxyphenol) N-methylcarbamate] was applied twice to the 4 control animals in November; later, rotenone was applied liberally and rubbed thoroughly into the hair coat twice in December (4 calves), once in January (2 calves), and once in early March (4 calves).

In 1982–83, one female and one male of the same treatment group were assigned to each observation pen; the 6 reference animals were maintained together in a larger pen. Each year throughout daylight hours a team of observers recorded behavioral data in 2.5 h intervals after which they were replaced by a new team. Each day, 6 moose were observed simultaneously: 4 treated animals, 2 each from the 21,000 and 42,000 tick treatments, and 2 controls. The remaining 6 moose, 4 treatments and 2 controls, were observed the following day; observations occurred 6 days/month. Behaviors were recorded for 60, 1-min intervals/h. If moose could not be observed in their entirety (e.g., behind trees or the shed), the interval was discarded from analysis. In October 1982, behaviors of infested moose were first recorded 16–20 days post-infestation. Observers were as consistent as possible with all trained similarly.

Within 1 week after each monthly observation period in 1982–83, ticks were removed from the 6 reference calves to measure and classify the developmental stage (see Addison and McLaughlin 1988). The 5 stages of development were: 1) October – larvae detaching, molting, and reattaching as unfed nymphs, 2) November to January – 100% nymphs with slow growth (diapause), 3) February – 90%

feeding nymphs, 10% feeding adults, 4) March – 50% feeding nymphs and 50% feeding adults, and 5) April – 90–100% feeding adults.

All studies were approved under an animal care protocol with close scrutiny by a provincial veterinarian who determined the April termination date each year. In most cases experimental moose were euthanized (see Addison et al. 1987) for related study of pathology and to collect and count the remaining ticks.

Three distinct behavioral activities were defined and measured during observations: grooming, rubbing, and shaking. Grooming was defined as the use of one body part applied to the same or other body part; antlers, ears, head, teeth, tongue, neck, and hind feet were used to groom. Rubbing was defined as the application of pressure against an extraneous object. Only vertical structures (fences, trees, shed) were available for rubbing in Year 1; slanted poles secured in each pen allowed moose to stand under or over the pole to rub their upper and lower body in Years 2 and 3. There were 5 distinct types of shaking: 1) the head, 2) the body, 3) head then body, 4) body then head, and 5) head and body simultaneously.

Most quantitative comparisons among grooming, rubbing, and shaking were restricted to year 3 when the data spanned the months from September (pre-infestation) to April, and 4 moose were in each treatment. Parts of the body to which grooms and rubs were applied are illustrated in Figure 1.

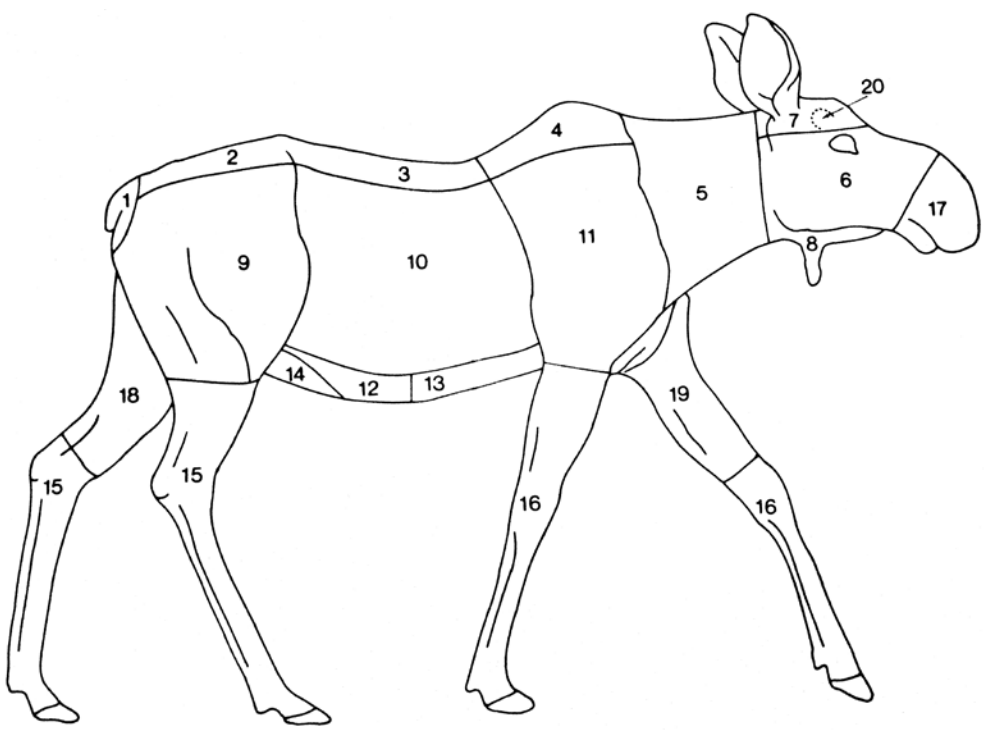

Fig. 1. Areas on moose for which grooming and rubbing were recorded (1-perianal; 2-croup; 3-back and loin; 4-withers; 5-neck; 6-sides of head; 7-forehead; 8-dewlap/chin; 9-thigh/upper hind leg; 10-ribs; 11-shoulder/upper foreleg; 12-posterior belly; 13-chest/anterior belly; 14-penis/scrotum; 15-hind feet and lateral hind leg; 16-forefeet and lateral foreleg; 17-muzzle/nose; 18-medial hind leg; 19-medial foreleg; 20-antlers).

The elapsed time of grooms and rubs was measured with a stopwatch (nearest second). If the beginning or end of an activity was not observed, length was assigned as equal to the monthly average of that activity.

Monthly rates of grooming for each moose were expressed as the number of distinctly different grooms/h and total minutes groomed/h. The grooming rate in a monthly observation period was calculated from the number of grooms and the average groom time, applying the average groom time to each groom for which length was unknown, summing a revised total groom time, and dividing it by the hours of available observation. Rates of rubbing were calculated similarly. The cumulative time of grooming plus rubbing was also calculated on a monthly basis.

Hair loss data from 1982–1983 were as described for these same moose by McLaughlin and Addison (1986). The cumulative volume of hair loss represents loss only on the dorsal and lateral aspects of the body behind the head; that is, the neck, withers, shoulders, back/loin, ribs, croup, thigh, and perianal areas (Fig. 1).

The number of ticks that survived through to detachment of engorged females was calculated by retrieving detached ticks from the pens plus counting the ticks remaining on each moose at the end of the experiment (see Addison et al. 1979). The pens were checked for ticks morning and evening throughout the adult female detachment period; one-half of the collected ticks were attributed to each of the 2 moose in each pen.

Data analysis

The Shapiro-Wilk normality test was used to assess the normality of data. Student's *t*-test was used to compare both the rate and duration of uninfested moose pre-infestation (September) and post-infestation (October). ANOVA was used to test for relationships between rate and duration of grooms among treatment groups during pre-infestation in September and post-infestation in October, as well as of rubs post-infestation. Spearman rank correlation was used to test the monthly relationship of mean grooms and mean rubs among all 5 treatment groups. Spearman rank correlation was used to test relationships between cumulative grooming-rubbing and hair loss, body weight at death, and total number of detached and remaining ticks at experiment end. ANOVA was used to test for differences in the mean rate of shakes by treatment in April. Sample size precluded testing for differences among monthly mean grooms plus rubs by treatment group.

RESULTS

After annual infestations, a total of 5006 h of observation occurred during the 3 years: ~50–110 h/moose/month from November to April in Year 1, ~35–50 h from October to April in Year 2, and ~27–30 h from October to April in Year 3. An additional ~17–23 h/moose of observation occurred prior to infestation in Year 3. Despite our efforts, some ticks transferred to certain control moose and remained on them throughout the experiments. An untreated control in Year 2 had plentiful ticks within its hair and was excluded from the analysis; no ticks were observed on the second control and it was not euthanized to digest hair and count ticks. In Year 3 when acaricides were applied, 1 control was tick-free and 4, 21, and 84 ticks were collected from the other 3 control animals.

Modes of grooming

A total of 25,429 grooms were observed of which 18,903 (74%) were identified to specific mode and area. Licking with the tongue and scratching with the hind feet were the predominant modes (82%). The tongue was used nearly exclusively (81–99%) to groom the perianal, croup, back/loin, ribs and thigh/upper leg areas; likewise, the hind feet were used to groom (~93%) the neck, cheek, forehead, and dewlap. Ears, antlers, teeth, and the neck curled back on itself with a pinching-like action were lesser modes of grooming (Table 1).

Modes of grooming varied among moose as certain animals groomed more with their teeth, head, ears, neck, and antlers (Table 1). Control moose groomed proportionally more with their hind feet than infested moose, and 2 controls groomed with their teeth, just 1–2 × each. Only the 10 moose infested with ≥20,000 larvae groomed with their teeth and ears (Table 1).

Areas groomed and rubbed

Moose with >20,000 larvae groomed most to the thigh and upper hind legs, ribs, shoulder, and upper forelegs, back and loin, neck, withers, and forefeet and lateral forearms (Table 2). Rubs were directed mainly to the head (34.8%), neck (33.9%), shoulder and upper foreleg (8.9%), and withers (7.8%) (n = 2479). Location of rubbing was distributed similarly among treatment groups except that the back/loin and withers were not rubbed by control moose. Control moose groomed proportionately more to the sides of the head, forehead, muzzle, feet, and lateral aspects of the limbs.

Grooming and rubbing were highest on the single infested side during the first post-infestation observation period for 2 of 3 moose (Table 3). Subsequently, <50% of grooms and rubs were on the infestation side at 1–2 months post-infestation and varied

Table 1. Grooming activity by infested (*Dermacentor albipictus*) and uninfested control moose, Algonquin Park, Ontario, 1980–1983. Control moose were accidentally exposed to a minimal number of ticks of unknown origin. Activity is described by groom total and proportionally by mode (body part used to groom). NA = not applicable, female.

Moose ID	Infestation (# ticks)	# grooms	Hind feet	Antlers	Teeth	Head	Ears	Tongue	Neck
M4	0	351	32.5	NA	0.3	6.2	0	61.0	0
M11	0	58	24.6	0	1.3	3.3	0	71.1	0
M12	0	252	28.2	NA	0	9.1	0	62.7	0
M17	0	108	28.1	0.8	0	9.9	0	61.2	0
M18	0	137	36.8	NA	0	6.6	0	56.6	0
M5	1000	450	23.8	0.8	3.1	1.1	0.2	69.3	1.6
M6	8000	1582	4.4	4.4	1.1	8.9	1.2	79.5	0.4
M1	20,000	1697	17.9	1.7	1.8	15.3	10.4	47.4	6.1
M9	21,000	844	19.5	0.1	1.1	2.1	0.4	76.8	0.1
M10	21,000	2095	14.6	NA	1.0	18.5	2.6	63.2	0
M13	21,000	912	13.3	0.3	0.3	2.4	1.6	82.0	0
M14	21,000	1157	15.8	NA	1.0	7.4	5.1	70.5	0.2
M3	22,000–23,000	3025	15.7	9.6	0.5	8.5	2.4	63.2	0
M7	42,000	2020	9.4	0.1	0.6	5.6	6.4	77.6	0.1
M8	42,000	995	15.0	NA	0.6	9.8	27.5	46.8	0.3
M15	42,000	1967	10.9	0.2	2.8	6.1	1.3	78.4	0.2
M16	42,000	1253	14.5	NA	1.4	2.6	2.0	79.6	0

Table 2. Distribution of grooming by infested (*Dermacentor albipictus*) and uninfested control moose, Algonquin Park, Ontario, 1981–1983. Control moose were accidentally exposed to a minimal number of ticks of unknown origin. Grooming activity per body location is described by average percent.

	Infestation treatment		
	0	20,000–23,000	42,000
# moose	5	6	4
# grooms	906	9730	6235
Grooming location			
Perianal (1)	1.1	3	3.2
Croup (2)	2.2	3.2	3.9
Back and loin (3)	9.1	11.1	9.7
Withers (4)	1.8	9	5
Neck (5)	4.3	10.2	5.9
Sides of head (6)	4.3	2	1.1
Forehead (7)	2.7	2	1.2
Dewlap/chin (8)	0.2	0.6	0.5
Thigh/upper hind leg (9)	14.8	12.6	15.8
Ribs (10)	14.3	11	11.5
Shoulder/upper foreleg (11)	3.9	10.5	12
Posterior belly (12)	2.8	2.7	5.3
Chest/anterior belly (13)	4	2.6	2.7
Penis/scrotum (14)	1.4	1.1	2
Hind feet/lateral hind leg (15)	9	5.1	6
Forefeet/lateral foreleg (16)	11.7	8.1	6.3
Muzzle/nose (17)	9.9	2	1.2
Hind leg-medial (18)	2.3	2.4	6.1
Foreleg-medial (19)	0.3	0.6	0.7
Antlers (20)	0	0.3	0.1

between sides thereafter. A higher proportion of grooms was on the infestation side during the first 4 months post-infestation for the third animal (Table 3).

Rates and duration

Moose groomed approximately 1–3 times/h in September prior to infestation and no differences were found among treatment groups ($P = 0.46$; Table 4). There was no difference in the rate of grooming ($P = 0.22$) or in the duration of individual grooms ($P = 0.14$) before and immediately after infestation in control moose, and their grooming activity (min/h) declined gradually from October to April (Table 5).

The number of grooms/h increased 2.4–5.3 fold immediately after infestation in moose with 21,000 larvae and 6.1–28.2 × in moose with 42,000 larvae (Table 4). Immediately following infestation, both grooms/h ($P = 0.002$) and duration of individual grooms ($P = 0.002$) were different among treatment groups. Grooming time (min/h) by moose with ≥21,000 larvae was stable or declined somewhat from November to January, generally increased in February and March, and was highest in April when adult ticks were feeding. Moose infested with 1000 and 8000 larvae in November had more variable rates of grooming through the infestation period. Mean time spent grooming was perfectly correlated with level of infestation from December through April ($R_s = 1$, $P = 0$; Table 5).

Table 3. Monthly percentage of grooms-rubs to the infested side of 3 moose treated with *Dermacentor albipictus*, Algonquin Park, Ontario, 1980–1983. Individual infestations were: Moose 1 – 20,000 ticks on 25–26 September; Moose 2 – 1000 ticks on 11 November; Moose 3 – 8000 ticks on 11 November. Only Moose 3 continued heavier grooming on the infested side for >1–2 months post-infestation (see bolded data).

Month	Moose 1 – R	Moose 2 – R	Moose 3 – L
October	**65.5**		
November	57.8	**63.4**	**72.7**
December	42.7	42.6	**73.5**
January	55.4	51.5	**65.3**
February	44.3	41.8	**61.6**
March	42.7	62.5	37.3
April	39.5	55.2	42

Rubbing did not follow a similar pattern as grooming. There was no difference in rubs/h among treatment groups ($P = 0.4$) shortly after infestation. Time spent rubbing was generally more variable than grooming, increased throughout the infestation period (Table 5), and was perfectly correlated with level of infestation in March and April ($R_s = 1$, $P = 0$) for moose with ≥8000 larvae.

The combined mean rate of grooming and rubbing (min/h) by treatment group was positively related to level of infestation every month during the period of infestation (Table 6). The mean maximum time spent grooming and rubbing was 7.65 min/h (13% of time) during April for the most heavily infested animals. Intense individual bouts of grooming and rubbing during April lasted 13–141 min with 0.72–1.62 different grooms - rubs/min. Differences in grooming and rubbing between

Table 4. Rate and duration of grooms by moose pre- and post-infestation with *Dermacentor albipictus*, Algonquin Park, Ontario, 1980–1983. Control moose were accidentally exposed to a minimal number of ticks of unknown origin.

Infestation	Moose ID	# grooms/h		Duration of grooms (sec)	
		Pre-infestation (Sept)	Post-infestation (Oct)	Pre-infestation (Sept)	Post-infestation (Oct)
0	11	0.9	0.6	11	10
	12	1.4	5.7	8	17
	17	1.4	0.9	10	7
	18	1.3	1.7	8	12
21,000	9	1.7	4.0	8	23
	10	3.0	13.2	7	17
	13	1.2	4.1	8	19
	14	1.2	6.6	6	19
42,000	7	1.8	16.3	6	31
	8	1.2	12.0	7	23
	15	0.7	18.3	5	22
	16	1.8	11.1	8	22

Table 5. Average of grooming and rubbing time (min/h) by infested (*Dermacentor albipictus*) and uninfested control moose, Algonquin Park, Ontario, 1980–1983. Control moose were accidentally exposed to a minimal number of ticks of unknown origin. *indicates the holding pens had no angular pole for rubbing back or belly; the other trials provided a pole.

	Infestation	# Moose	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr
Grooms	0	4	0.23	0.54	0.20	0.34	0.12	0.11	0.11	0.09
	1000*	1			0.11	0.34	0.52	0.42	0.16	0.21
	8000*	1			0.06	0.47	1.36	1.67	0.66	2.53
	21,000	4	0.21	2.21	2.42	2.03	1.76	1.94	1.74	2.91
	42,000	4	0.17	5.92	3.78	3.05	2.88	4.02	3.77	5.71
Rubs	0	4	0.108	0.022	0.044	0.017	0.004	0	0.004	0.016
	1000*	1			0.006	0.021	0.021	0.004	0	0.017
	8000*	1			0.06	0.1	0.07	0.06	0.12	0.5
	21,000	4	0.032	0.124	0.018	0.091	0.174	0.252	0.185	0.714
	42,000	4	0.069	0.024	0.831	0.689	1.489	1.419	1.623	1.939

Table 6. Average time (min/h) of combined grooming-rubbing by infested (*Dermacentor albipictus*) and uninfested control moose, Algonquin Park, Ontario, 1980–1983. Control moose were accidentally exposed to a minimal number of ticks of unknown origin.

Infestation	# Moose	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr
0	4	0.34	0.56	0.24	0.36	0.12	0.12	0.12	0.11
21,000	4	0.24	2.33	2.44	2.12	1.93	2.19	1.93	3.63
42,000	4	0.24	5.94	4.61	3.74	4.36	5.44	5.39	7.65

control moose and moose with 1000 larvae were minimal (Table 5). The animal with 8000 larvae groomed and rubbed more from January to April than that with 1000 larvae (Table 5). The amount of hair loss was positively correlated to the estimated cumulative grooming-rubbing calculated at 197 d post-infestation in April (R_s = 0.86, P = 0.0003). However, the amount of cumulative grooming-rubbing to realize 2% hair loss was highly variable among moose; ~ 34–81 h for 6 moose and 102 and 204 h for 2 others.

Tick recovery

The number of ticks recovered after daily searches of the pens and boiling hides was 0–85 for control moose, 1522–4565 for 4 moose infested with 21,000 larvae, and 2102–8535 for moose infested with 42,000 larvae (Table 7). The number recovered was not related to cumulative grooming-rubbing in moose infested with 21,000 (R_s = −0.8, P = 0.2) or 42,000 larvae (R_s = −0.4, P = 0.6); however, the recovery estimates should be considered minimal because our protocol could not account for detached ticks consumed by ravens (*Corvus corax*) and Canada jays (*Perisoreus canadensis*). The minimum proportion of the infestation dose surviving to detachment varied from 5–22% (μ = 12.4%).

Body weight relationships

The 6 males weighed 200–273 kg at the end of the 1982–1983 experiment, but weight of individuals was not related to the

Table 7. Relationship between cumulative grooming-rubbing time and hair loss on infested (*Dermacentor albipictus*) and uninfested control moose, Algonquin Park, Ontario, 1980–1983. Control moose were accidentally exposed to a minimal number of ticks of unknown origin. Hair loss was calculated as in McLaughlin and Addison (1986) at 187 days post-infestation. Recovered ticks were those removed from animals euthanized on 18–29 April plus detached ticks collected daily in holding pens.

Infestation	Moose ID	Grooming-rubbing (min)	Hair loss (%)	# Ticks recovered
42,000	15	19,723	26.1	2102
	7	9061	30.4	5016
	8	6862	25.7	8535
	16	6417	27.9	4721
21,000	10	6310	23.6	1522
	14	5659	27.2	1933
	9	3255	24.3	2731
	13	2800	0.8	4565
0	12	834	4.7	21
	17	489	0	0
	11	487	0	85
	18	426	0	4

cumulative time spent grooming and rubbing ($R_s = -0.6$, $P = 0.21$). At the absolute scale, the 3 heaviest males (224–273 kg) groomed and rubbed the equivalent of 2.5 days (average over daylight hours) throughout the study, whereas the 3 lightest (200–217 kg) groomed and rubbed an average of 17 days (>7 × more). One male infested with 21,000 larvae was an outlier as it groomed minimally compared to other infested animals. Conversely, body weight of the 6 females (174–237 kg) was related to the cumulative time spent grooming and rubbing ($R_s = -0.81$, $P = 0.05$). The 3 heaviest females (216–237 kg) groomed and rubbed an average of only 3.6 days (daylight hours) in contrast with the 3 lightest (174–198 kg) that groomed and rubbed an average of 12 days.

Shaking

Of the 3328 shakes recorded, ~80% were of the body or head alone. The rate of shaking (shakes/h) did not consistently increase immediately after infestation, but occurred much more frequently during April for moose infested with ≥21,000 larvae. Significant differences ($P = 0.04$) in the mean rate of shaking (shakes/h) occurred in April: control (μ = 1.23, 0.67–1.68); 21,000 larvae (μ = 2.96, 2.39–3.93); 42,000 larvae (μ = 3.54, 2.39–6.21).

DISCUSSION

Winter ticks are associated with increased grooming and rubbing by moose (Glines and Samuel 1989, Samuel 1991, Welch et al. 1991, Mooring and Samuel 1999) and free-ranging wapiti (*Cervus canadensis*) (Mooring and Samuel 1998b). Our controlled study with captive moose is the first to document grooming and rubbing by moose across a specific range of winter tick infestation. Specifically, we found a positive relationship between infestation level and the extent of grooming and rubbing by captive calves.

The fact that control calves groomed and rubbed less frequently through the winter (1982–1983) reflected, in part, the repeated application of acaricides to prevent accidental infestations of larvae. However, we were unsuccessful in completely eliminating all winter ticks and advise that effective treatments be mandatory during translocations of moose to prevent geographic spread of ticks. Wild moose presumably harbor light infestations of winter ticks without overt behavioral response and/or hair loss, since grooming and rubbing was generally similar between control moose and those infested with 1000 larvae. The threshold for discernibly increased grooming and rubbing by moose was no more than 8000 larvae.

As expected, we found that grooming and rubbing were consistently highest in March-April during the feeding stages of nymphs and adult ticks (Samuel 1991, Welch et al. 1991, Mooring and Samuel 1999). Grooming began within minutes of infestation and remained elevated for 2–3 weeks during the period of feeding, detachment, and ecdysis by larvae and their subsequent reattachment as nymphs. Early grooming by moose was also observed by Welch et al. (1991) but not by others working with both captive and free-ranging wild moose (Samuel 1991, Mooring and Samuel 1999). This discrepancy might simply reflect the timing of observations as the latter studies commenced post-larval feeding. Further, our consolidated infestation scheme did not reflect the normal, weeks-long infestation period (Mooring and Samuel 1999) and may have contributed to an enhanced level of irritation and grooming activity in the study moose.

Unlike grooming, rubbing increased only in March-April when adult ticks were feeding, as reported by others (Samuel 1991, Mooring and Samuel 1999). Although patterns were evident, the individual variation in the amount and modes of grooming and rubbing varied extensively within infestation treatments. Possible explanations include differences in immunological sensitivity and/or ticks redistributing themselves on the body. Despite variation in behavior and response among moose in this and other studies, it is clear that the level of grooming and rubbing by moose is influenced by the phenology and feeding by winter ticks.

For 2 of 3 moose infested on only one side of their body, grooming and rubbing was greater on the infested side for only the first month, post-infestation. This short period is consistent with newly ecdysed nymphs which are mobile in the hair coat and redistributed themselves prior to the November observation period (see Addison and McLaughlin 1988). Similarly, nymphs ecdysing to adults would be mobile and able to redistribute themselves.

A positive relationship between grooming-rubbing and hair loss in moose has been reported previously (Glines and Samuel 1989, Mooring and Samuel 1999), and our study animals were used by McLaughlin and Addison (1986) in their study of hair loss on tick-infested moose. We calculated cumulative grooming-rubbing during daylight hours only because we observed no grooming-rubbing activity during limited nocturnal observations in January. However, we believe that this behavior likely occurs continuously during the intense period of irritation in March-April, and consider the cumulative grooming-rubbing estimates as minimums. The combined results of this study and that of McLaughlin and Addison (1986) clearly document that infestation level has a strong and direct relationship with both cumulative grooming-rubbing and hair loss during the latter part of the infestation period.

Importantly, extensive grooming and rubbing occurred earlier in the infestation period prior to measurable hair loss. Thus, the timing of hair loss surveys (as an indirect measure of infestation level and mortality) is an important consideration and should be conducted late in the infestation period, and always at the same time in the phenology of ticks. Our results support the approach of Bergeron and Pekins (2014) and others who have used annual hair loss surveys in late winter and early spring to estimate tick infestation among areas and years.

Shaking was considered separate from grooming and rubbing because hair is not removed from the follicles or sheared, hence it had little effect on differential hair loss between infested and uninfested moose. Nevertheless, the higher rate of shaking by infested moose was consistent with shaking as a response to ticks. Although Geist (1963) noted that moose shook frequently following exposure to water, neither rain nor snow explained the difference in shaking between infested and control moose as all treatment groups were observed simultaneously under the same weather conditions. Shaking was also included as a form of grooming in previous studies (Samuel 1991, Mooring and Samuel 1999).

Proposed previously (Glines and Samuel 1989), here we document for the first time the negative relationship between cumulative grooming-rubbing and tick infestation on moose. Many factors contribute to the proportion of ticks removed during infestation including the marked individual variation in modes of grooming that we observed, and that these modes varied in relative effectiveness. In addition, grooming continues where ticks and most hair have been removed because the sheared off, embedded mouthparts of ticks continue to irritate moose. Despite some detached ticks burrowing into the duff layer or being removed by ravens and Canada jays (Addison et al. 1989) before we could retrieve them, the majority (77–96%) of ticks originally infested on moose and not present in late April likely were removed by grooming and rubbing.

Blood extraction by ticks is considered a serious threat to the physiological condition of young moose in late winter and early spring (Samuel 2004, Musante et al. 2007), as are potential thermoregulatory impacts from hair loss (McLaughlin and Addison 1986, Addison and McLaughlin 2014). Most physiological influence from blood loss and thermoregulatory challenges would occur in late winter-early spring after nymphs engorge in February (see Addison and McLaughlin 1988). Thus, the lower body weight of infested calves in late autumn and early winter (Addison et al. 1994) presumably reflects their higher rates of grooming, rubbing, and immunological response. Indirectly, our data also support the acute physiological response and high mortality measured in calves harboring on average >45,000 adult ticks in spring (Jones et al. 2019), an adult infestation level exceeding our original larval treatments.

In summary, moose with higher infestation of winter ticks groomed and rubbed more than other moose over a range of infestation from 8000–42,000 larvae. Increased grooming and rubbing lead to increased hair loss in our infested moose, although considerable variation in the amount and modes of grooming and rubbing existed among moose. In general, these results validate use of hair loss surveys among years or areas as potential measures of variation in the infestation level of winter ticks on moose.

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