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Some Behavioural And Physiological Responses Of Free - Ranging Moose (Alces alces) To Infestations Of Winter Ticks (Dermacentor albipictus)

by

Patricia Marie Skorupka ©

A thesis submitted to the Faculty of Graduate Studies and Research in partial fulfillment of the requirements for the degree of Master of Science

in

Department of Biological Sciences

Edmonton, Alberta

Fall 1999

0-612-47097-0

University of Alberta

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The undersign certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled Some Behavioural And Physiological Responses Of Free - Ranging Moose (Alces alces) To Infestations Of Winter Ticks (Dermacentor albipictus) submitted by Patricia Marie Skorupka in partial fulfillment of the requirements for the degree of Master of Science.

William M. Samuel

William M. Samuel

Jens Roland

Jens Roland

Robert J. Hudson

Dated: June 7, 1999

This thesis is dedicated to

Kitty, who gave me the freedom to try,
Dr. LeBaron Carlton Colt III, who gave me the confidence to do it,
Trish, who believed I should
And
Lisa for her understanding and patience.

ABSTRACT

Grooming behaviour of moose in Elk Island National Park, Alberta, infested with winter ticks, Dermacentor albipictus, were described, quantified and compared with behaviour of experimentally infested moose from a previous study. Concomitantly, a manipulative experiment using wild moose, some of whom were treated with ivermectin to reduce tick numbers, was conducted in the Park to examine effects of ticks on aspects of moose nutrition. Results showed that moose groom most in September and March and April, when tick larvae and nymphs and adults, respectively, were feeding on blood. Tick - grooming behaviours of free - ranging and captive moose were the same, but wild moose groomed less than captive moose. Tick - induced grooming was negatively correlated with feeding activity, suggesting that moose sacrifice feeding time to remove ticks. This and the physiological stress caused by feeding ticks, likely compromised energy reserves of moose in late winter - early spring.

Acknowledgements

Research aspects of this study were funded by Elk Island National Park and the Natural Sciences and Research Council of Canada (NSERC) (grants to W. M. Samuel) and a Canadian Boreal Alberta Research grant to me from the Canadian Circumpolar Institute. I received financial support from the Department of Biological Sciences, University of Alberta (Graduate Teaching Assistantship and bursary), Canadian Federation of University Women (bursary), University of Alberta Access (bursary), and NSERC (W. M. Samuel).

Trapping and radio - collaring wild moose takes a huge effort and many members of Elk Island National Park Warden Staff and Maintenance Division provided that for me. I am grateful to all who were involved, especially Norm Cool who provided technical expertise and logistical support needed to trap and radio collar moose and who helped with many other technical matters concerning moose at the Mud Lake facility. Rob Kaye, Wes Olson, Dennis Madsen, and Brent McDougal were always available to squeeze (pun intended) the token American into their busy schedules.

I am especially grateful to my hard - working and enthusiastic field technician, Cedric Gerrard, who willingly took on 'other duties as assigned' and provided moral support at the 'Back Alley'. Cedric contributed greatly to the success of this research. I am likewise indebted to Phil McLaughlin, Dallas Kaiser and Lee Rueb who spent many cold hours collecting snow urine and faecal pellets and videotaping moose. My heartfelt thanks also to the many volunteers and friends who, from time to time, assisted in various ways with this project. Without intending to slight anyone, I wish to particularly thank Francis Reintjes, Ainsley Sykes, Karen Yee, Rachael, Tony Gaboury and Don Page.

Some materials and services used in the Mud Lake study were generously provided by Jim Harbidge, Merck Agvet, ivermectin boluses and

balling guns, Dr. Robert Jones, Uncas Veterinary Clinic, placebo boluses and injectable saline, Bob McClymont, Fish and Wildlife Services, and Elk Island National Park, autopsies of Mud Lake moose.

I wish to thank my supervisor, Dr. William Samuel, for providing me the opportunity to participate in tick research and for his support throughout my master degree program. Dr. Samuel's willingness to share his ideas about winter ticks helped shape the direction of my research, and his advice and insightful criticisms contributed greatly to the development and completion of this thesis.

I thank Dr. Jens Roland and Dr. Robert J. Hudson for their willingness to serve as members of my supervisory committee. I greatly appreciate the help I received from them and several others who also gave freely of their time to assist me in various ways. Dr. Alan Shostak and Dr. Roland help on statistical matters, Dr. Hudson and Norm Cool, Elk Island National Park, provided critical reviews of physiological data, Dr. Jan Murie advised on animal behaviour and Trefor Higgins, Dynacare Kasper Medical Laboratories, provided technical advise on assay procedures.

A special thank you goes to Dr. Sandra Zohar for her support and encouragement through this study.

Last, but definitely not least, I thank my daughter Lisa Duff, my Dad and family members and friends for their support and patience. In particular I wish to express my appreciation to my brother, Glen Marsella and good friend, Patricia Gates, who generously allowed me the use their e - mail and faxing services, respectively, and Dr. Robert Howe, Suffolk University, Boston Massachusetts, for his continued interest in my academic career.

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CHAPTER 1

INTRODUCTION

All vertebrates host a variety of internal and external parasites. They respond to the presence of these organisms with a variety of defences, most notably immune and behavioural responses. From a behavioural perspective, Hart (1990) listed five strategies used by vertebrates to defend themselves against macroparasites (i. e., arthropods and helminths) :

"1) avoidance or removal of parasites;
2) controlled exposure to parasites to potentiate the immune system;
3) behaviour of sick animals including anorexia and depression to overcome systemic febrile infections;
4) helping sick kin or group mates; and
5) sexual selection for mating partners with genetic endowment for resistance to parasites."

The first strategy, avoidance or removal of parasites, includes host grooming as a behavioural means to remove parasites. Grooming is a regularly performed behaviour used by many mammals (Hart 1994). It serves several important functions including promotion and strengthening of social bonds and reduction of tension and aggression among primates during social gatherings (Woolridge 1982; Hart 1990). Grooming can also serve as a 'comfort movement' (Geist 1963) to clean and condition the hair coat, thus, retaining its protective and insulatory functions, (Borchelt 1980; Woolridge 1982; Patenaude and Bovet 1983) and to remove ectoparasites (Hart et al. 1992; Mooring et al. 1996).

If one accepts that grooming behaviour provides a selective advantage for its host; i. e., functions in controlling numbers of ectoparasites (Hart 1992), it is necessary to show (1) "that the parasite in question has a detrimental effect on host fitness" and (2) "the behaviour must be effective in helping the animal avoid or remove the parasite in question." Ixodid ticks are one group of parasites that fit the first criterion. They are obligatory, blood - sucking parasites of domestic and wild animals. These ticks not only remove much blood (a single unfed adult female tick can process 4000mg of host blood, (Kaufman 1989), but they also secrete pharmacological agents, anticoagulants, enzymes and toxins that facilitate the blood - feeding process (Binnington and Kemp 1980; Kaufman 1989). The results for hosts can be quite costly. This is well documented for tick - infested cattle, which suffer reduced weight gain due to blood loss and tick - caused anorexia (O'Kelly and Seifert 1969; O'Kelly et al. 1971; Norval et al. 1988, 1989).

Specific to the present study is the known detrimental effect of winter ticks, Dermacentor albipictus, for moose (Alces alces). Epizootics of winter ticks have been implicated in the morbidity and mortality of moose (Cowan 1951; Berg 1975; Samuel and Barker 1979; Addison and Smith 1981; Blyth and Hudson 1987; Garner and Wilton 1993). Specifically, at least five die - offs of moose in Elk Island National Park (EINP) have been associated with major infestations of winter ticks since 1933, with peak infestations likely to have occurred in 1933, 1937, 1948, 1968 and 1981 (Blyth 1995). Preliminary evidence that many moose were infested with overwhelming numbers of ticks during the 1981 - 1982 die - off was provided by Samuel and Welch (1991). They reported mean numbers of ticks over 40,000 during 1981 - 1982.

Captive moose experimentally infested with winter ticks suffer from anaemia and other physiological effects, reduced fat reserves, reduced growth (in calves), restlessness and extensive grooming and hair loss (Glines and Samuel 1984, 1989; McLaughlin and Addison 1986; Samuel et al. 1986; Samuel 1991; Addison et al. 1994; also see Welch et al. 1990 and Addison et al. 1998). In addition, immune complex disease and specific changes in blood chemistry indicative of liver damage possibly due to tick toxins, have been reported for captive moose (Glines and Samuel 1989). Energy costs associated with alopecia and inclement weather were thought to be responsible for some of the lower fat levels (McLaughlin and Addison 1986). However, Welch et al. (1990) found that during a mild winter, tick - induced hair loss did not affect fasting metabolic rates or weight changes of captive moose. They concluded that extensive hair loss on moose during March and April probably imposed a nominal thermoregulatory cost.

There are other potential costs associated with grooming, such as loss of water from saliva and excessive attrition of the dental comb, loss of time from foraging, resting, and vigilance for predators (Hart 1990, 1992; Mooring and Hart 1995).

That grooming is effective in removing ticks has been well demonstrated in studies in which animals were prevented from oral grooming. For example, the number of Boophilus microplus on cattle restrained from grooming increased almost four - fold compared to unrestrained cattle (Snowball 1956; Bennett 1969). African Impala (Aepyceros melampus) fitted with a harness to prevent self grooming had a median of 20 times more female ticks than unrestrained impala (Mooring et al. 1996). Results of research on captive moose experimentally infested with winter ticks suggest that intense grooming during March and April removes many female ticks before completion of the normal blood meal (Drew 1984; Drew and Samuel 1989; Welch et al. 1991). Glines and Samuel (1989) recovered 74% of the infestation dose of winter ticks from a moose calf with no hair loss and 32% from a calf with severe hair loss. They suggested that moose that groom and develop extensive hair loss remove the most ticks. The conclusions reached by these studies were based on relative measurements of tick removal such as reductions in the yield (Drew 1984) or weights (Welch, et al. 1991) of engorged adult ticks. The direct effect of grooming by moose in controlling or reducing numbers of winter ticks is not known.

Tick - induced destruction of the winter hair, which is often extensive for moose (Samuel and Welch 1991), coincides with the developmental life - stages of the winter tick (Samuel 1991). Although captive moose groom soon after being infested with winter tick larvae in October (Samuel 1991; Welch et al. 1991), hair damage (which generally occurs first on the side of the neck; Samuel et al. 1986), usually begins in January (Glines and Samuel 1984). As the frequency and duration of grooming increases, concomitant with blood feeding of larval, nymphal and adult ticks (Samuel 1991; Welch et al. 1991), areas of increasing hair damage and loss are seen on the neck, shoulder, withers, chest, flank, back and perianal region (McLaughlin and Addison 1986; Samuel et al. 1986). By the end of April hair damage and loss is extensive and often involves > 80% of the lateral torso (Samuel et al. 1986) (Figure 1-1).

In Alberta, winter tick infestation is highly seasonal and development of the parasitic life - stages on moose occurs at predictable times (Glines and Samuel 1984; Drew and Samuel 1985, 1989; Samuel 1988). Moose in EINP acquire larval - stage winter ticks from vegetation continuously from early September through mid - November (Drew and Samuel 1985). (Larvae cluster at the tips of vegetation awaiting contact with a passing moose.) Within approximately 3 weeks of transmission, larvae feed on moose blood, moult to the nymph instar and enter morphogenetic diapause (Drew and Samuel 1989). During January, February and March, nymphs become active and take a blood meal and moult to adults. Adult males and females feed on moose blood during March and April. However, only female ticks engorge on blood; male ixodids feed intermittently and take small blood meals (Oliver 1989). By May, females disengage from moose and drop to the ground where they seek shelter in the

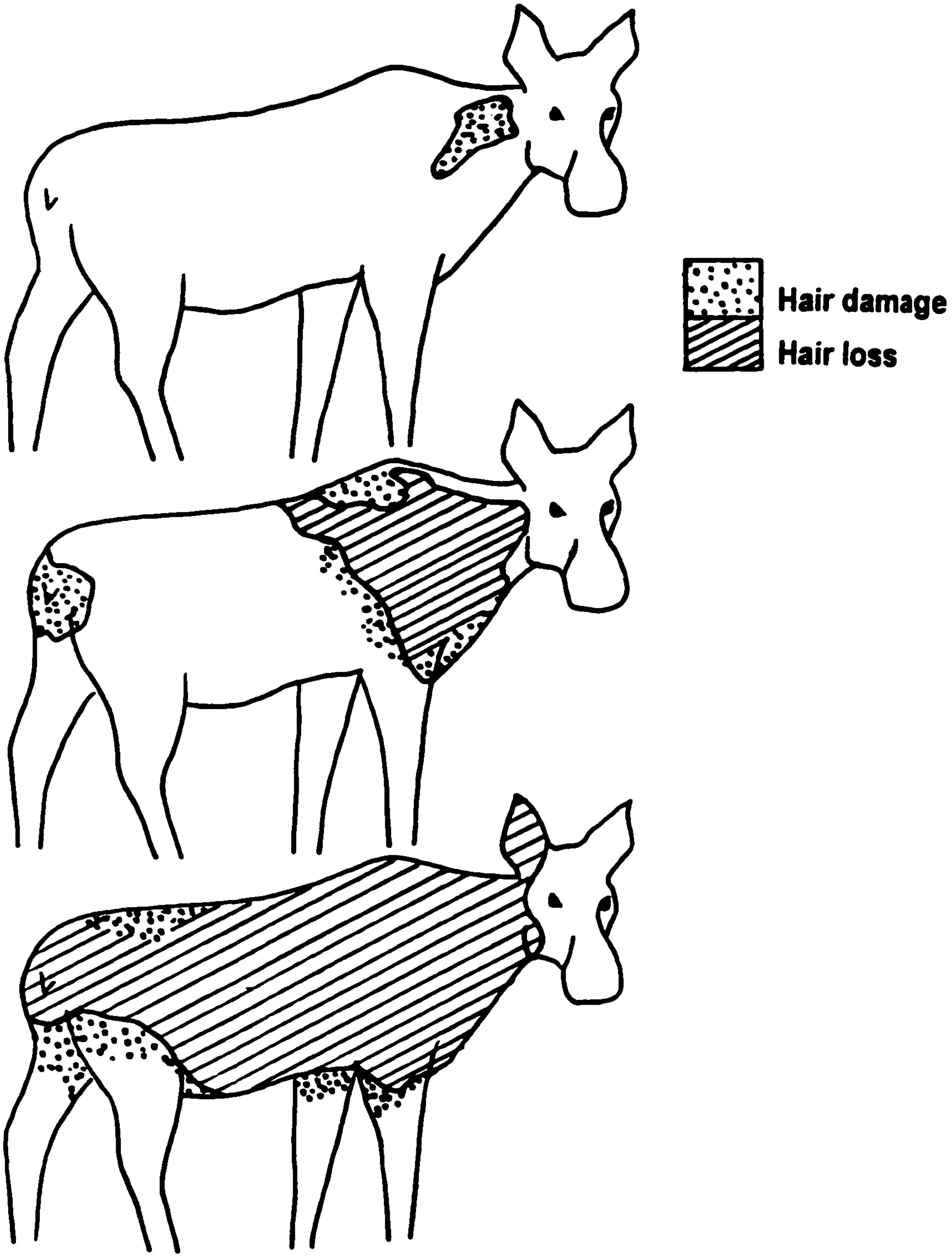

Figure 1-1 Sequence and progression of hair damage and loss as a result of tick - induced grooming by moose. (Figure adapted from Samuel and Barker 1979)

leaf litter. In June, females lay their eggs and die (Drew and Samuel 1986). Eggs hatch in mid - August - early September. Shortly thereafter, larvae ascend vegetation (Drew 1984) and the cycle begins again.

Moose divide their time fairly evenly between resting, foraging and ruminating (Risenhoover 1986, 1987; Renecker and Hudson 1989; VanBallenberghe and Miquelle 1990; Gillingham and Klein 1992). During winter, moose in Alberta spend ~ 10 h/d feeding and ~ 13 h/d resting, of which ~ 11h is spent ruminating (Renecker and Hudson 1989). The remaining hour is allocated to miscellaneous activities such as standing, walking, eating snow or drinking water, running and grooming. In Isle Royale National Park (ISRO), Michigan, resting and foraging - related activities dominate winter time - budgets of moose as well (Risenhoover 1987). Moose there allocate 30 min/d to other activities, such as grooming, alert behaviour, social interaction and movement; i. e., running and walking not associated with foraging. Only 10 min/d during winter is spent in other activities by moose in Denali National Park and Preserve (Risenhoover 1987). The small percentage of time moose spend in activities that are not directly related to the acquisition or conservation of energy suggest that any factor that disrupts foraging, ruminating or resting is detrimental to moose.

It is thought that winter ticks negatively influence activity patterns of moose. Risenhoover (1987) noted that as tick - infested moose on ISRO spent more time grooming, they spent less time foraging. Samuel (1991), in trying to explain why tick - infested moose spent less time lying down than did tick - free moose, suggested that intense irritation, presumably caused by feeding ticks, may be involved. In direct contrast, Glines and Samuel (1989) postulated that fatigue associated with tick - caused anaemia could prevent moose from travelling the distances required to find sufficient food.

If ticks do indeed interfere with feeding and resting - rumination time, the nutritional consequences could be severe for moose, especially during late winter - early spring when moose are often nutritionally and energetically stressed. Increase rumination time could limit forage intake (Risenhoover 1986). Any further reduction in forage intake (beyond that which normally occurs due to reduced availability and quality of winter forage, Schwartz et al. 1984, 1988; Renecker and Hudson 1986) would exacerbate winter weight loss and further increase energy deficits. Alternately, the 'itch' caused by feeding ticks could affect food choices of moose. Highly agitated moose might eat whatever food is at hand rather than select the most nutritious browse or they might clip twigs beyond the current annual growth. Older twigs or twigs browsed at greater diameter contain fewer nutrients (Cowan et al. 1950; Hjeljord et al. 1982).

EINP provides an excellent opportunity to study moose in a natural setting. Moose there are accustomed to people, movement in and out of the Park is prevented by a game fence and all moose are assumed to be infested with D. albipictus. Long - term Park studies, from 1977 to present, provide records of prevalence and progression of hair loss and numbers of ticks on moose, data which can be compared with results of the present study and published data from captive studies. Thus, during winters 1994 -1995 and 1995 -1996, I studied moose in the Park, conducting the first field study of the behavioural responses of moose to infestations of winter ticks.

The purpose of my study was to determine temporal patterns in tick - induced grooming by moose to test the following predictions: (1) tick - caused grooming activities peak in frequency and duration when the parasitic life stages (larvae, nymph and adult) are feeding on blood, (2) the resulting destruction of the winter hair coat each year is positively correlated with the yearly population size of winter ticks, (3) nutritional status of moose is lowered because foraging activities are sacrificed to grooming, particularly during March and April when adult ticks are feeding, and (4) grooming is effective at removing ticks. To accomplish this, the behavioural responses of free - ranging moose to tick challenge were observed; results were compared to those from captive studies and with long - term unpublished data from the Park (Chapter 2). In addition, behavioural observations of several moose outfitted with radio collars, some of whom were treated with ivermectin to remove ticks, were made (Chapter 3). My goals were to determine differences in feeding, resting and ruminating activities, diet quality and nutritional status of moose with and without ticks. Faecal samples were collected and analysed for nitrogen and lignin content. Urine samples were collected from snow to determine the influence of winter ticks on body condition.

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CHAPTER 2

Some behavioural aspects of grooming by moose (Alces alces) in response to naturally acquired infestations of the winter tick (Dermacentor albipictus)

INTRODUCTION

The winter tick (Dermacentor albipictus) is common on wild ungulates, particularly members of the family Cervidae, throughout the southern two - thirds of North America. Although all North American members of the Cervidae are infested, moose (Alces alces) are the most important and severely affected hosts (Welch et al. 1990, 1991). Die - offs of moose associated with winter ticks are common (Berg 1975; Samuel and Barker 1979; Addison and Smith 1981; Garner and Wilton 1993). Dead and dying moose are found in poor and weakened condition with hair damage or loss often exceeding 50% of the lateral torso and infested with large numbers of winter ticks (Samuel and Barker 1979; Samuel and Welch 1991). In some die - offs, numbers of moose lost are significant; often hundreds of heavily tick - infested moose are found dead (Berg 1975; Samuel and Barker 1979; Addison and Smith 1981; Garner and Wilton 1993).

Growth and development of winter ticks on moose in Canada (Addison and McLaughlin 1988 and as summarized by Lankester and Samuel 1997) follow a predictable annual pattern (Drew and Samuel 1985, 1989; Samuel 1988; Welch et al. 1991). Eggs hatch into larvae from mid - August through early September. Larvae ascend vegetation within 2 weeks of hatching (Drew 1984) and are available for transmission to moose continuously from early September through November. Larvae blood - feed on moose within ~ 3 weeks, moult to nymphs and enter a resting state (morphogenetic diapause) that varies in duration between ~ 40 - 200 days. Nymphs feed and moult to adults between January and March. Adult females begin to engorge in late February and continue through the end of April.

One outcome of winter tick infestation on moose is grooming (Samuel 1991). Grooming serves an important function in removing ectoparasites, including ticks, from both domestic and wild animals (Snowball 1956; Murray 1961, 1987, 1990; Bell et al. 1962; Lewis et al. 1967; Bennett 1969; Brown 1971; Barker et al. 1990; Hart 1990, 1992, 1994; Hart et al. 1992; Mooring 1995; Mooring and Hart 1995; Mooring et al. 1996; Mooring and Samuel 1998a, b, c, 1999), and it "may involve any number of actions by the host to dislodge and remove a pest; i. e., scraping, rubbing, licking, skin quivering, tail tossing, soil and water bathing, etc." (Barker et al. 1990).

The time invested in grooming by experimentally infested captive moose is considerable (Samuel 1991) and coincides with blood - feeding by the parasitic life stages, larvae, nymphs and adults. Intensive grooming begins during the nymphal feeding period in January and steadily increases in frequency and duration to March - April (Samuel 1991) when adult ticks engorge on blood.

Licking/biting and rubbing are the predominant grooming behaviours used by captive moose (Samuel 1991).

Increased grooming during times when ticks blood – feed was observed for naturally tick - infested wild moose (Mooring and Samuel 1998a, 1999). Although wild moose had high densities of immature ticks from October through February, the frequency of grooming was very low until adult females began to feed in March and April.

Samuel (1991) recorded time spent grooming by captive moose, but Mooring and Samuel (1998a, 1999) did not. This is unfortunate, because frequency and duration can give different and complimentary pictures of the same behaviour (Altmann 1974; Martin and Bateson 1993). For example, the frequency of grooming by captive moose increased 1.3 times from the end of October (when tick larvae are feeding on blood) to January (when nymphs begin to feed), but duration of grooming increased 2.1 times (Samuel 1991). Thus, it would be desirable to report both the frequency and duration of grooming by moose, and to do so during the entire phase of tick infestation on moose; i. e., September to May. Unfortunately, Samuel (1991), Welch et al. (1991) and Mooring and Samuel (1998a, 1999) did not begin their observations until 30 October, 20 October and 1 October, respectively.

A major result of grooming by moose is destruction and premature loss of the winter hair coat (McLaughlin and Addison 1986; Samuel et al. 1986). Samuel and Welch (1991) found that 89% of 724 moose from 9 populations had hair damage or loss attributable to winter ticks. In one population, near Rochester in central Alberta, the mean annual percent hair damage or loss exceeded 50% of the lateral torso in 3 of 13 winters (Samuel and Welch 1991). Loss is most severe at winter's end when, in the wild, many moose are on a low plane of nutrition and energy reserves are often nearly exhausted. Thus, it is probably safe to assume that extensive grooming and destruction of the hair coat is costly to moose.

An obvious benefit of the time and energy invested by moose to grooming is the removal of ticks. Unfortunately, this aspect of winter tick biology has only been studied indirectly; i. e., the conclusion that grooming reduces numbers of winter ticks on moose is based on comparisons between the severity of tick - induced hair loss on captive moose infested with winter ticks and the relative proportions of tick life stages (Glines and Samuel 1989) or reductions in the yield of engorged females ticks (Drew 1984) collected from these animals. Results of Welch et al. (1991) suggest that moose are not as efficient as white - tailed deer, mule deer or elk in removing ticks; however, there has been no attempt to determine the number of ticks removed during grooming.

Because of the lack of data on the extent of winter tick - induced grooming by wild moose, and the possibility that results of Samuel (1991) for captive moose are not applicable to wild moose, I conducted a 2-year field study in Elk Island National Park. Major objectives were to: 1) determine the frequency and duration of tick - induced grooming behaviours used by moose, 2) evaluate the efficiency of grooming as it relates to reduction in tick numbers and 3) determine the degree of association between annual hair damage and tick numbers. Because grooming is a common behavioural pattern of moose, especially when winter ticks engorge on blood, I predicted that there would be a positive correlation between the amount of hair and numbers of ticks removed by grooming. I also predicted that there would be a positive correlation between mean annual percent hair loss and mean annual tick numbers on moose.

METHODS

Description of Study Site

The study was done in Elk Island National Park (EINP) (Figure 1) from September 1, 1994 - April 30, 1995 and September 1, 1995 - April 30, 1996 (often referred herein as Year I and Year II, respectively). EINP is located approximately 40km east of Edmonton, in the Beaver Hills area of central Alberta, Canada (53° 37′N, 112° 52′W). The Park contains 195km^2 of aspen parkland and is bisected by Highway 16 (Figure 2-1). The Main Park unit of 136 km^2 is located north of Highway 16 and the smaller unit of 59km^2 is south of the highway. The south unit, known as the isolation area, is used primarily as an enclosure for wood bison (Bison bison athabascae). Both Park units are enclosed by a 2.2m - high game fence that limits the dispersal of large ungulates.

The region has a northern mid - latitude continental climate (Olson 1985). Winters are cold and dry and summers are warm and wet. Average annual

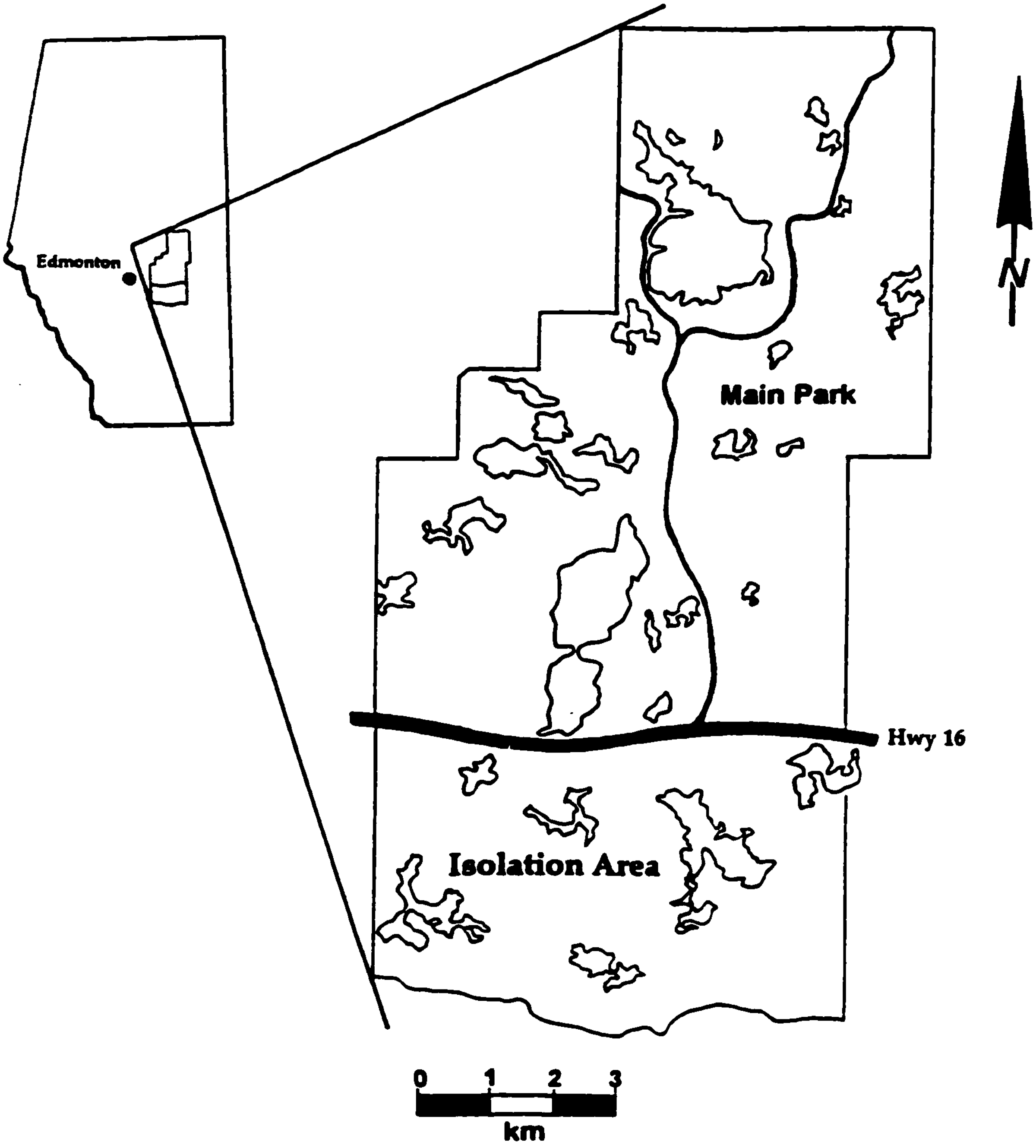


Figure 2-1. Map of Elk Island National Park, Alberta. (Map courtesy of Parks Canada)

precipitation is 487mm, of which 22% occurs as snow (Blyth 1995). Mean daily temperature during winter is -10.6° C. Extreme winter minimum and maximum temperatures ranging from -50 to 0° C (Olson 1985). Snow begins to accumulate when mean daily temperatures fall below freezing, usually around 16 November and persists to ~17 March (Olson 1985). Average annual snowfall at EINP is 106mm (Blyth 1995).

EINP is situated on the northern portion of the Cooking Lake glacial moraine, which rises 30 to 60m above the general level of the surrounding plains. Surface till deposited by the last glacial advance formed an undulating complex of small hills and closed depressions that comprise the major landforms of the Beaver Hills. Topography within the Park consists of a mosaic of small hummocks, prairie mounds and linear ridges with some interspersed flat lying glaciolacustrine areas (Jennings 1984). Several large shallow lakes, small ponds, bogs and seasonal sloughs are interspersed between the small hills and ridges.

Vegetation in the Park consists of aspen forest interspersed with open grasslands and wetlands. The dominant tree species are quaking aspen (Populus tremuloides), balsam popular (Populous balsamifera) and white birch (Betula papyrifera) (Schultz and Bentz 1992). Several patches of white Spruce (Picea glauca) are present also. "Beaked hazelnut (Corylus cornuta) is the most important understory shrub and tends to form a closed canopy approximately 1.3m high, especially under aspen" (Cairns and Telfer 1980). Prickley rose (Rosa acicularis), wild sarsaparilla (Aralia nudicaulis), pea vines (Lathyrus ochorleucus and *L. venosus*) and bunchberry dogwood (*Cornus canadensis*) are other common shrub species (Cairns and Telfer 1980). Willows (*Salix* spp.), sedges (*Carex* spp.), cattails (*Typha latifolia*), sphagnum and black spruce bogs (*Picea mariana*) dominate the wetlands. Grasslands vary in composition, but Kentucky bluegrass (*Poa pratensis*) and smooth brome (*Bromus inermis*) are common species.

Estimated fall populations of moose in EINP for 1994 and 1995 were 383 and 369, respectively (Ecosystem Status Report, 1994). Moose are habituated to humans because of frequent contact with Park visitors through the year. Other large mammals are elk (*Cervus elaphus*), white - tailed deer (*Odocoileus virginianus*), mule deer (*Odocoileus hemionus*), plains bison (*Bison bison bison*), wood bison (*Bison bison athabascae*) and coyotes (*Canis latrans*).

Although moose observed in this study were not examined for winter ticks, I assumed that all were infested and that the behaviours observed were against ticks, not other parasites, because: (1) all of 114 moose examined by Samuel and Welch (1991) from EINP, 1977 - 1990, were infested with *D. albipictus*, (2) each of 98 additional moose from other sites in western Canada, 1980 - 1990, were infested with *D. albipictus* (Samuel and Welch 1991), (3) mean densities of winter ticks on moose from EINP are very high and usually exceed 1.00 ticks/cm^2 (Samuel and Welch 1991), (4) no other ectoparasite occurs on moose from EINP (Samuel, unpubl.) and (5) hair loss patterns observed annually for moose in EINP are spatially and temporally identical to those observed in captive studies in which moose were experimentally infested with winter ticks (McLaughlin and Addison 1986; Samuel et al. 1986; Glines and Samuel 1989). In addition, all of 63 elk examined from EINP, 1980 - 1996 (Samuel and Welch 1991; Mooring and Samuel 1998b) were infested as were all of eight moose hides from EINP examined by me, 1995 - 1996.

Data Collection

Grooming Behaviour

Moose were located in the main and isolation areas of the Park by driving Park and boundary roads early in the morning and late in the afternoon. Restricted - access roads leading to bison handling facilities, elk traps or Warden's residences were travelled also. Moose were observed from a vehicle, sometimes using 10x binoculars depending on ground cover and viewing distance to moose. Often two or more moose, mostly cow - calf pairs, were observed simultaneously. The distinctive shape and size of the dewlap and hair loss patterns (mid-winter to early spring) served to identify moose and to avoid repeated observations of the same individual within a 24h period.

Moose were observed as long as they remained in view; however, I later extracted the first 15min of an observation period in order to quantitatively analyze grooming and activity data and to calculate % of observation time moose spent grooming. Grooming behaviours, licking (a. k. a., oral grooming), rubbing, scratching or shaking (Samuel 1991) and activity states were recorded during

15min focal animal sampling periods. (As defined by Altmann (1974), 'focal animal' sampling is the recording of all behavioural activities of an individual animal during a specific amount of time.) Age (calf or adult) and sex of each focal animal were recorded also.

"Behaviours may be regarded as either events or states" (Altmann 1974). They essentially lie at opposite ends of a continuum of behavioural patterns. An event of grooming is a relatively brief behaviour pattern such as scratching. The prominent aspect of grooming events is their frequency of occurrence per unit time. For example the number of times a moose scratches in 15min would be a measure of the frequency or rate of the behavioural event of scratching. Frequencies of grooming behaviours from each 15min observation were extrapolated to mean number of events/h for all moose observed. Duration of grooming; i. e., the total length of time all events of a particular behaviour lasted during a 15min sampling period, was recorded also. These measurements were extrapolated to mean s/h for moose that groomed.

States are behaviour patterns of more appreciable duration such as grooming or foraging (Altmann 1974; Martin and Bateson 1993). The critical aspect of a state is its duration, such as the total time a moose spends grooming during a 24h period. I recorded the following activity states: grooming, feeding, resting, ruminating and other activity; i. e., alert behaviour, standing idle or chewing, moving, drinking water or eating snow and social interactions. Transition times (i. e., the beginning and end of each activity state and event of grooming) were recorded in the sequence in which they occurred. This provided information on the time moose spent in various activities, thus, enabling me to sample behavioural states at 2min intervals (instantaneous sampling method, see Altmann 1974; Martin and Bateson 1993). Instantaneous samples were transformed to percent total monthly scans.

Data were summarized by month and by duration of the three parasitic instars of winter ticks on moose. Because tick larvae in EINP are available for transmission to moose as early as the first week of September (Drew and Samuel 1985) and feed within 21d of attachment (Drew and Samuel 1989), I considered 1 - 14 September as a part of the tick attachment period, and 15 - 30 September as part of larval feeding. Except for larval feeding, predominant parasitic tick feeding periods were categorized following those of Welch et al. (1991) and are: 15 September through October, larval feeding; November - December, nymphal diapause; January - February, nymphal feeding and March - April, adult feeding.

Data from events of ear twitching were recorded; however, because of the fact that fly - repelling behaviour has not been associated with tick - induced grooming, events of ear twitching were not included in the frequency and duration data.

There were no significant differences between Years I and II in frequencies of grooming ($\underline{F} = 2.838$, $\underline{p} = 0.118$), duration of grooming (MWU, $\underline{p} = > 0.05$), percent activity scans (MWU, $\underline{p} = > 0.05$) and percent of observation time spent grooming (MWU, $p = 0.757$). Thus, data for each of these measures were combined.

Hair Damage and Loss

In order to assess hair damage and loss caused by grooming, diagrams were made on a moose silhouette. Areas of hair damage and loss were drawn and later converted to percentage surface area of the lateral torso of moose using a digitizing program, Sigma Scan Summa Sketch Plus. Usually only one side was drawn, but if both sides of a moose were drawn, the mean percent surface area was calculated. Winter ticks are the only known cause of the characteristic pattern of premature, sequential damage to, or loss of, winter hair on moose (see Figure 1, Samuel 1989).

Percent hair loss (from digitizing) observed on moose after 15 April and tick data from the present study (Chapter 3) were combined with similar data collected from moose in EINP between 1978 - 1990 (Samuel, unpubl.; Samuel and Welch 1991) to determine if changes in tick infestations correlated with hair loss. All moose had either died or were shot by Park wardens. Methods used to examine hides are in Chapter 3.

Dislodged Hair and Ticks

Beginning in mid - February and continuing to snowmelt in April, after watching a moose groom, I walked to the specific site where the moose had been standing or bedded when observed grooming and collected guard hairs, clumps of hair, and ticks. Specific grooming sites were located by following moose tracks in the snow and using physical references, such as a downed tree or a particular arrangement of trees or shrubs. Hair and ticks were picked by hand from the snow surface. Engorged female ticks lying on the surface of the snow were not collected because it could not be determined if they disengaged from the moose or were dislodged by grooming. Hair was collected also from branches of saplings and shrubs and from the bark of trees against which moose rubbed. Samples of hair and ticks were placed in individual plastic freezer bags and brought to the University of Alberta.

Hair samples were placed on paper towels and allowed to dry at room temperature. Clumps of hair were teased apart and examined for ticks using a dissection scope. Ticks were counted and aged (nymphs, engorged nymphs, male and female adults and engorged adult females); however, I did not attempt to differentiate between partially and fully engorged female ticks. Hair samples were then weighed on a Mettler AT261 Delta Range digital scale. Only three hair samples, each of which consisted of a few individual guard hairs, and no ticks were collected in Year II, so Year II was excluded from the analysis.

Statistical Analysis

Tick populations are typically non - normally distributed on host populations (Petney et al. 1990). Thus, most data were analysed using non -

parametric procedures (Zar 1984). The only exception were mean frequency data that were analysed using a general linear model analysis of variances (ANOVA), because of the possibility of interaction effects of years, grooming behaviours and among tick life - stages. Comparisons among mean duration of grooming by behaviour groups and tick - life stages were by Kruskal - Wallis one - way analysis of variance (ANOVA) or Mann - Whitney test. Non - parametric multiple comparison testing was used to determine differences among groups. Significant interaction effects of mean frequency data were compared using Bonferroni multiple comparison testing. Correlation analysis between 1) dislodged hair (g) and numbers of dislodged ticks, 2) time spent grooming and dislodged ticks and hair, 3) mean annual percent hair loss and mean annual numbers of ticks and 4) activity scan samples was by Spearman rank - order correlation. Because I predicted that the correlations between hair and ticks removed by grooming, and between annual percent hair loss and tick numbers on moose would be in a positive direction, one - tailed tests were used. Probabilities of 0.05 were considered significant. Means are reported with standard error (± SE) unless otherwise noted.

RESULTS

Overview and Grooming Behaviour

A total of 620 moose were observed during 768h of observations during the study (Table 2-1). Observations ranged in length from 1 to 168min. A total of

Table 2-1. Summary of moose observations in Elk Island National Park during September - April, Years I (1994 - 1995) and II (1995 - 1996).

	Year I	Year II	Total
Number of moose observed	312	308	620
Total hours observations	365	403	786
Number (%) of moose that groomed	95 (30)	92 (30)	187 (30)
Number of grooming events	370	301	671
Number of moose observed 15 min	159	158	317
Number (%) of these moose that groomed	37 (23)	48 (30)	85 (27)
Number of grooming events	69	118	187

187 moose (30%) were observed grooming and those moose performed 671 events of grooming (mean number of grooming events = 3.6 ± 6.2 SD). Correspondingly, 15min observations extracted from the initial data sets resulted in data for 317 moose. Eighty - five (27%) of these moose groomed and those moose performed 187 events of grooming (mean number of grooming events = 2.2 ± 2.1 SD). Total time spent grooming was 3,015s (mean s grooming = 35.5 ± 88.5 SD).

Moose used four grooming behaviours: licking, rubbing, scratching and shaking plus an apparent fly - avoidance behaviour, ear twitching. Licking involved a rapid series of biting-type movements and use of the tongue. Hair was occasionally seen on the tongue, lips and mouth of moose engaged in licking behaviour during March and April. Licking occurred while moose were standing or bedded and was delivered to the rump, flank, back, shoulder, chest, abdomen, thigh and perianal region.

Rubbing by moose consisted of three separate behaviours: use of the head to rub various parts of the body, use of antlers to rub various parts of the body and rubbing various parts of the head and body against vegetation. Head - rubbing consisted of vertical movements of the side of the head against the body. Rubbing with antlers involved turning the neck and twisting the head until the tip of the antler came into contact with the body. The head was then moved either from side to side or up and down in a series of short rapid movements. Antlers were used to rub their flank, rump and back. Moose used their head to rub their flank, rump, back and foreleg. Moose used the upper portions of their body, primarily the shoulder, neck and flank and areas of the head (in particular the side of the face, underside of the chin, back of ears and forehead) to rub against standing or downed trees bent at a 45^0 angle, saplings and erect brushy shrubs. Moose positioned themselves against the vegetation and moved the portion of the torso or area of the head to be rubbed in either a vertical or horizontal plane. Bedded moose rubbed the side of their face, underside of the chin, and forehead against shrubs and downed trees at the perimeter of their beds.

Moose scratched using the hoof of the hind leg. The leg was raised until the hoof came into contact with the body. The raised leg was then moved in a short rapid downward stroke which caused the hoof to scrape against the body. At the end of each stroke the sequence of movements was repeated. An event of scratching usually involved several rapid series of downward strokes delivered to the back of the ear, side of the face or neck, flank and abdomen. Moose primarily scratched themselves while standing, but on one occasion a moose calf scratched its neck and the top of its head while bedded.

Moose used three similar but distinctive shaking behaviours: shaking of the head shaking, shaking of the body and combinations of shaking both head and body. Head shaking involved moving the head from side to side in a horizontal plane. During body shaking the head and neck were held parallel to the ground and the hind legs spread slightly apart. Shaking began at the withers and shoulders and then spread throughout the torso terminating at the rump. The same side to side motion used for shaking the head was used to shake the body. During an event of head and body shaking, moose shook their head and then their body. Occasionally, moose performed the sequence in reverse. Moose shook their body while standing and their head when standing or bedded.

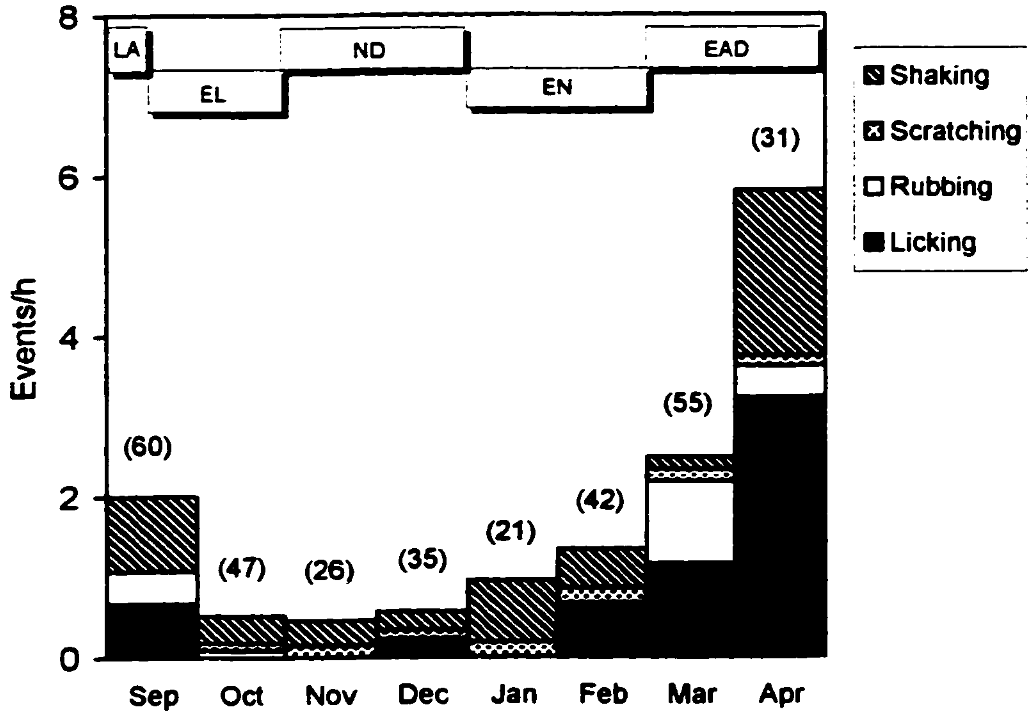
Although most grooming behaviours could be, and were, long in duration, shaking seldom exceeded 3s duration.

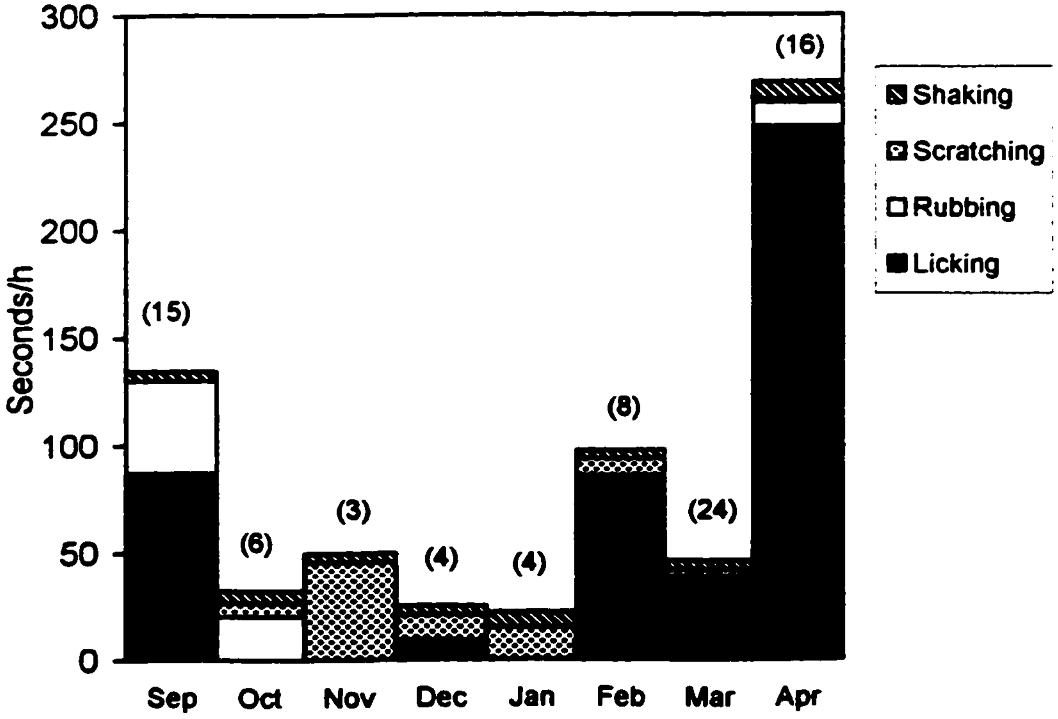
Ear twitching involved rotating one or both ears backward and forward in a vertical plane. The movement was rapid and was performed as a single event or a series of events. Twitching of the ears was observed during September, February, March and April. During March and April ear twitching intensified and was often performed in association with defensive grooming behaviours. Ear twitching is a common fly - repelling movement, and has been reported for domestic livestock, small mammals (Edman and Kale 1971; Harvey and Launchbaugh 1982; Harris et al. 1987; Hart 1992, 1994). Renecker and Hudson (1990) listed ear twitching as one of three movements by moose to indicate insect harassment.

Frequency and Duration of Grooming

Between September and April, moose groomed an average 1.3% (± 0.8) of observation time. The mean total frequency and duration of grooming was 2.4 (± 0.3) events/h and 141.9 (± 38.4) s/h, respectively. By month, grooming (all

Figure 2-2. Summary of frequency (mean number of events/h) and duration (mean s/h) of grooming behaviours by free - ranging moose from Elk Island National Park assumed to be infested with the winter tick (Dermacentor albipictus). Intervals of tick life stages were: 1 - 14 September = attachment by larvae (LA); 15 September - 31 October = feeding by larvae (= engorged larvae, EL); 1 November - 31 December = diapaused nymphs (ND); 1 January - 28 February = feeding by nymphs (= EN) and 1 March - 30 April = feeding by adults (EAD). Numbers in parentheses = number of moose observed (events data) and number of moose that groomed (duration data).


8
6
4
2
0
Events/h
LA
EL
ND
EN
EAD
(60)
(47)
(26)
(35)
(21)
(42)
(55)
(31)
Sep
Oct
Nov
Dec
Jan
Feb
Mar
Apr
Shaking
Scratching
Rubbing
Licking


300
250
200
150
100
50
0
Seconds/h
(15)
(6)
(3)
(4)
(4)
(8)
(24)
(16)
Sep
Oct
Nov
Dec
Jan
Feb
Mar
Apr
Shaking
Scratching
Rubbing
Licking

behaviour types combined) was more frequent in September, and March - April, than from October to February (Figure 2-2). By tick life - stage, the rate at which moose groomed (all behaviour types combined) was significantly different (F = 3.690, p = 0.035). Frequency of grooming in March and April, when nymphal and adult ticks were feeding on moose blood, was significantly different (Bonferroni, p = 0. 035) from November - December when nymphs were not feeding (Figure 2-2).

There were significant differences in the frequency of the individual grooming behaviours (F = 7.458, p = 0.004) used by moose (Figure 2-3). Although licking and shaking were the predominant behaviours, only the rate of shaking was significantly different from rubbing (Bonferroni, p = 0.015) and scratching (Bonferroni, p = 0.011). Interactions effects between frequency of grooming among the different behaviours and tick life stages were not significant.

Duration of grooming (all behaviour types combined) was concentrated in September, when larvae were attaching and in April, when adult ticks were feeding (Figure 2-2). Licking predominated. Differences in the duration of grooming behaviours were significant (KW, p = 0.001, N = 80). Of the four behaviours, duration of shaking was different from duration of licking (Q = 7.9), rubbing (Q = 4.6) and scratching (Q = 4.1). (Figure 2-4).

In terms of activity budgets based on instantaneous sampling at 2min intervals, feeding dominated the daily activities of moose from September - April

Figure 2-3. Mean (± SE) number of events/h (frequency) of winter tick - related grooming behaviours by moose in Elk Island National Park, 1994 - 1996. Intervals of tick life stages were: 1 - 14 September = attachment by larvae (LA); 15 September - 31 October = feeding by larvae (= engorged larvae, EL); 1 November - 31 December = diapaused nymphs (ND); 1 January - 28 February = feeding by nymphs (EN) and 1 March - 30 April = feeding by adults (EAD).
(number of moose observed)

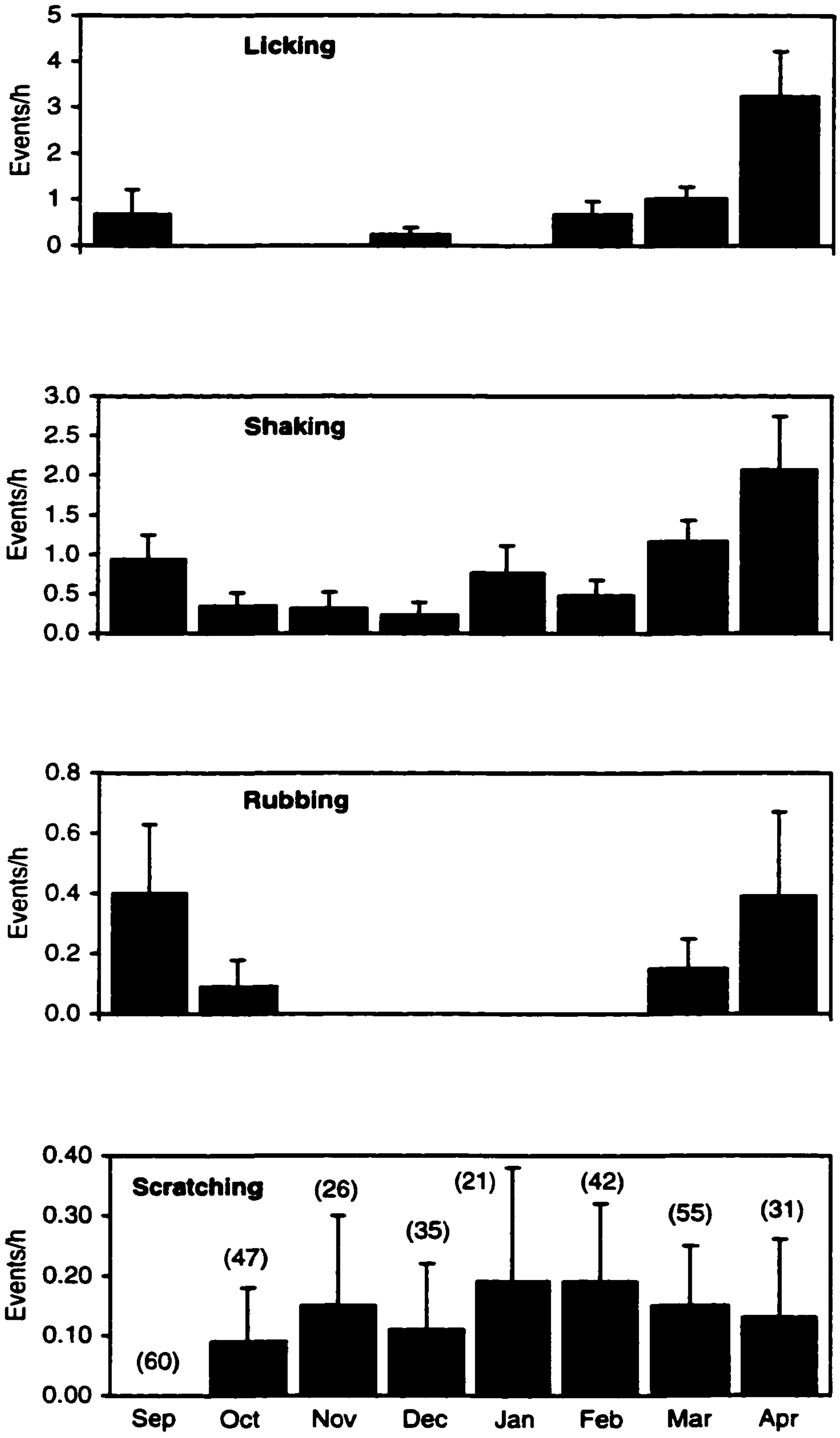
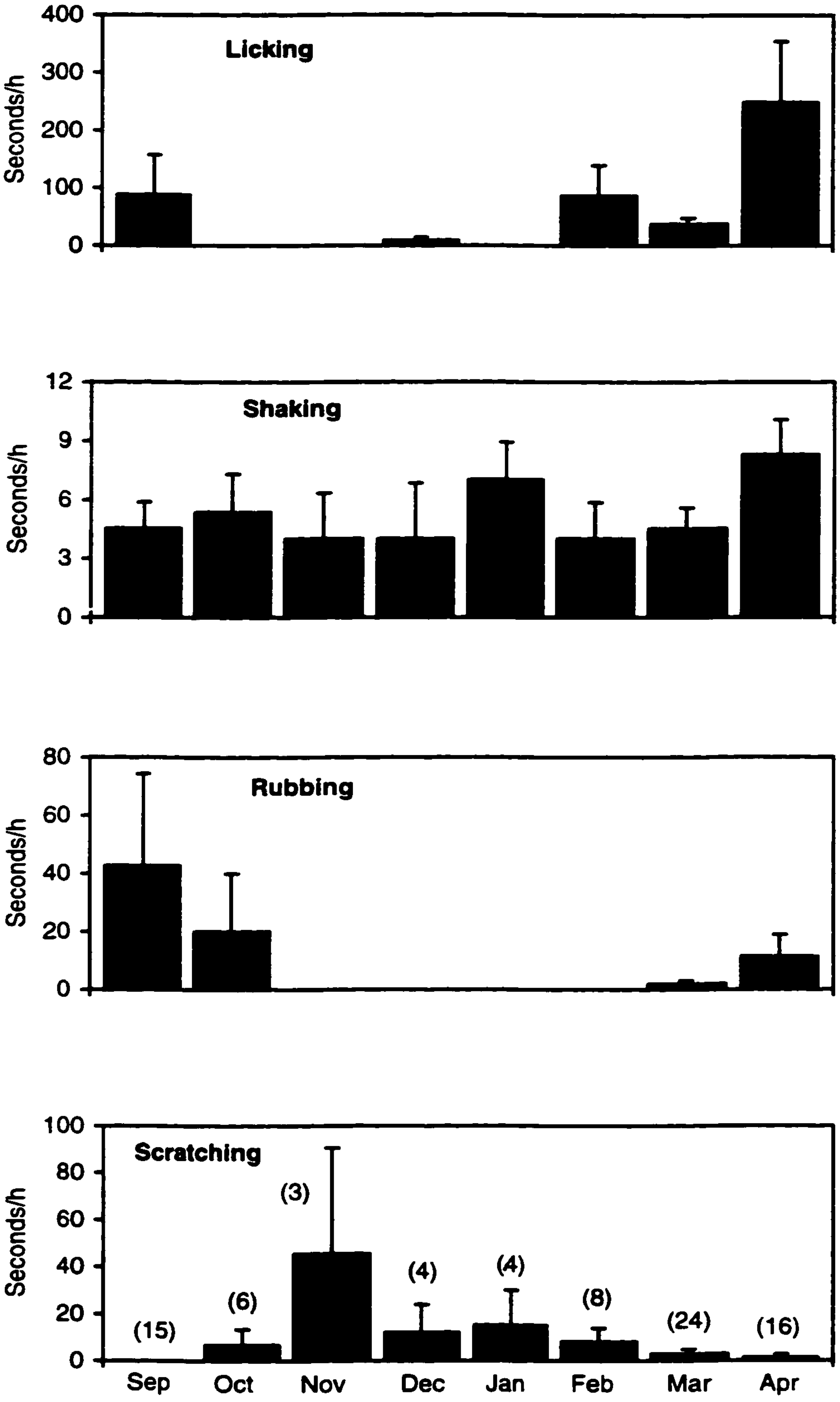

Licking
Events/h
5
4
3
2
1
0
Shaking
Events/h
3.0
2.5
2.0
1.5
1.0
0.5
0.0
Rubbing
Events/h
0.8
0.6
0.4
0.2
0.0
Scratching
Events/h
0.40
0.30
0.20
0.10
0.00
(60)
(47)
(26)
(35)
(21)
(42)
(55)
(31)
Sep
Oct
Nov
Dec
Jan
Feb
Mar
Apr

Figure 2-4. Mean duration (± SE) of winter tick - related grooming behaviours by moose in Elk Island National Park, 1994 - 1996. Intervals of tick life stages are: 1 - 14 September = attachment by larvae (LA); 15 September - 31 October = feeding by larvae (= engorged larvae, EL); 1 November - 31 December = diapaused nymphs (ND); 1 January - 28 February = feeding by nymphs (EN) and 1 March - 30 April = feeding by adults (EAD).
(number of moose that groomed)


Licking
Seconds/h
400
300
200
100
0
Shaking
Seconds/h
12
9
6
3
0
Rubbing
Seconds/h
80
60
40
20
0
Scratching
Seconds/h
100
80
60
40
20
0
(15)
(6)
(3)
(4)
(4)
(8)
(24)
(16)
Sep
Oct
Nov
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Feb
Mar
Apr

(Figure 2-5). Regarding tick - induced grooming, more time was spent grooming (all behaviour types combined) in March and April (percent scans 6.518, respectively), when adult ticks were feeding on blood, than during any other month (Figure 2-5). Significant negative correlations were found between percent scans feeding and (1) percent scans grooming (all behaviour types combined) (r_s = - 0.70, p = 0.05) and (2) the main specific behaviour, licking, (r_s = - 0.71, p = 0.05) (Figure 2-6). Time spent ruminating was very low (≤ 1.6%) except for February and March when percent scans ruminating was 22%, and 20%, respectively.

Dislodged Hair and Ticks

Seventeen grooming sites, areas where moose were either bedded or standing when observed grooming, were visited in March and April (Table 2-2). A total of 417 ticks, assumed to be dislodged by grooming, were recovered from seven sites. A total of 50.7g of dislodged hair was collected from 13 sites. No dislodged ticks or hair were found at four sites. Most (391) of the recovered ticks came from one site where a bull moose removed 44.4g of its hair coat during 22 min of constant grooming. This moose had no observable hair damage or loss at the beginning of the observation period but 9% of the surface area of the lateral torso was damaged or destroyed at the end of the observation period. Over half (54%) of the ticks removed from this moose were unengorged adults, 38% and 8% were engorged and unengorged nymphs, respectively.

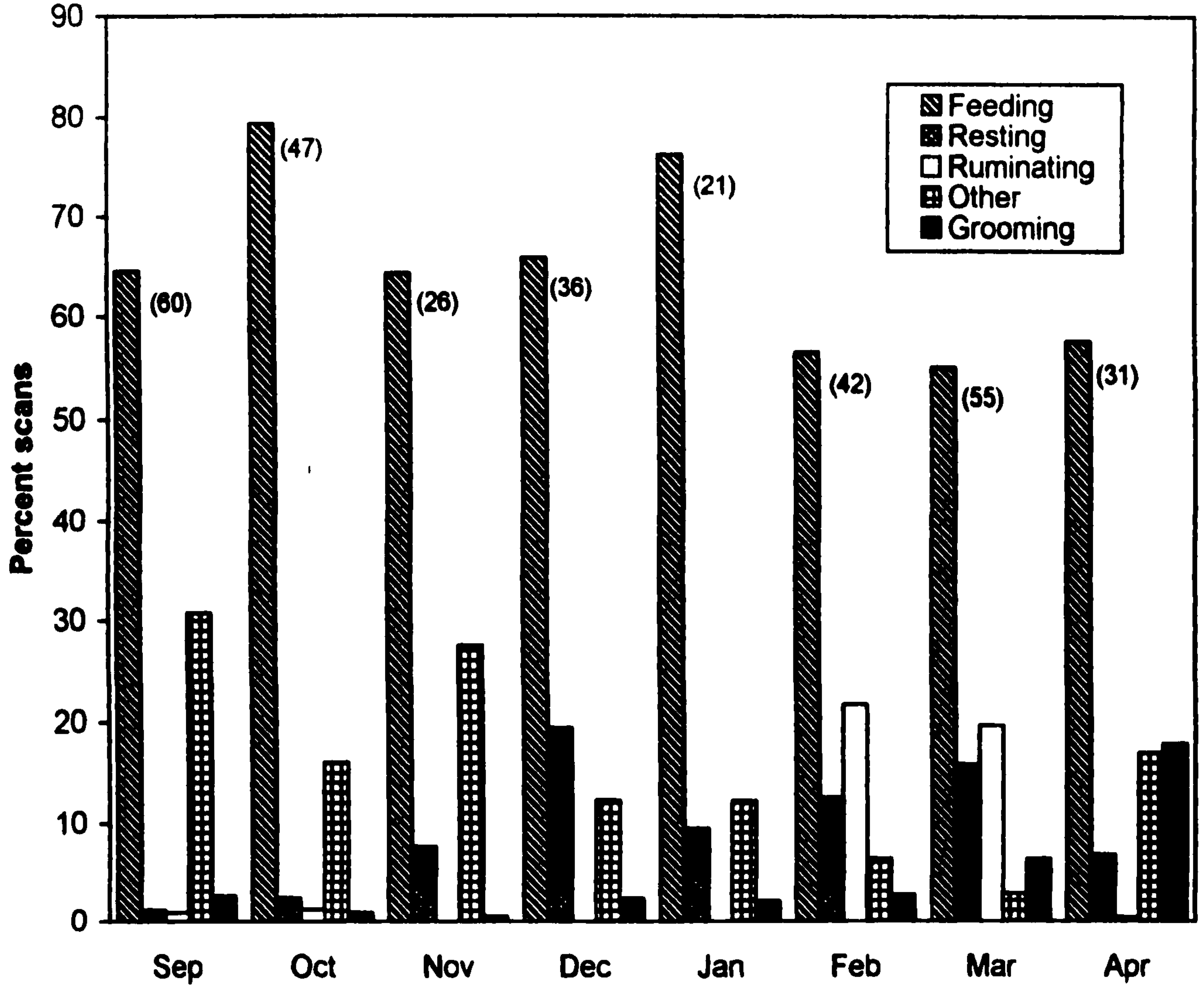

Figure 2-5. Percent activity scans for moose in Elk Island National Park, 1994 - 1995.

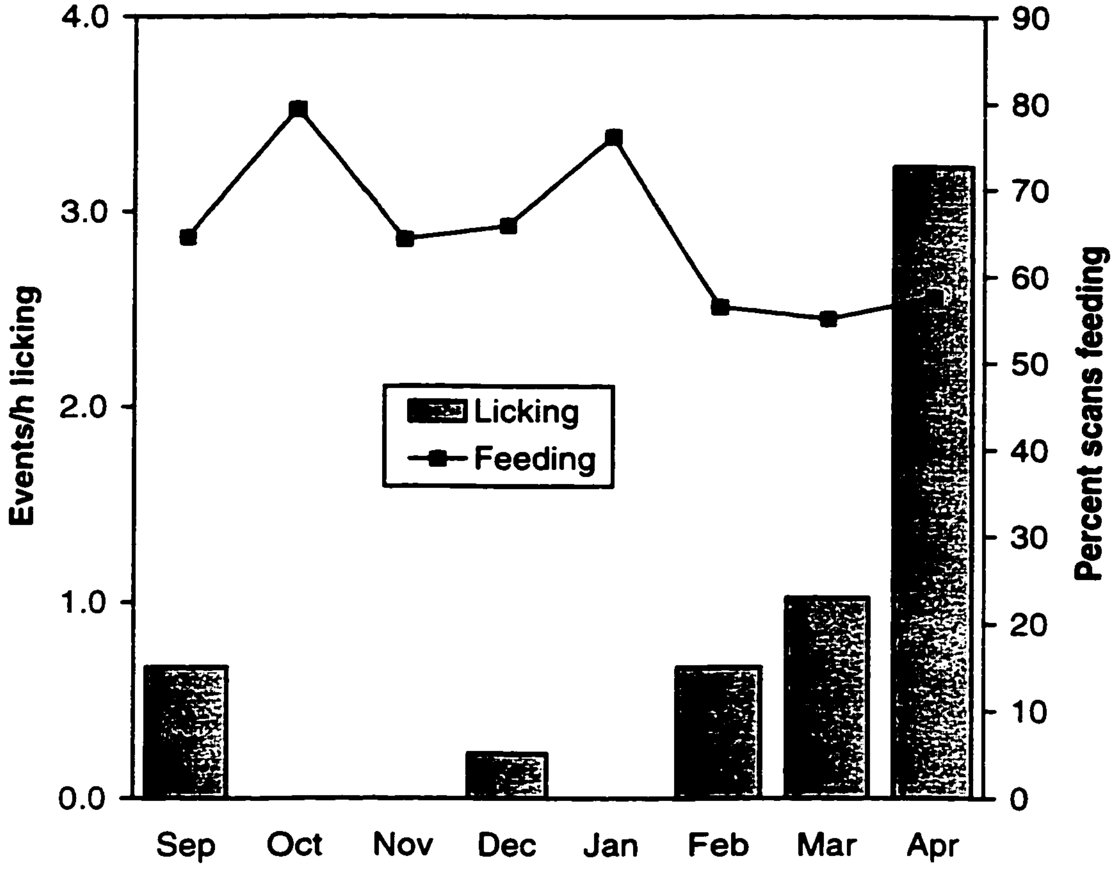

Figure 2-6. Percent scans feeding and mean events/h of licking by moose in Elk Island National Park, 1994 - 1996. Sample sizes and SE (for mean events/h licking) are on Figure 2-2.

Table 2-2. Weights of dislodged hair and numbers of winter ticks (Dermacentor albipictus) collected where 17 moose were observed grooming in Elk Island National Park during March and April, 1995.

Age/Sex	Date collected	Wt. of hair (g)	Numbers of ticks collected UN*	EN*	ADM*	ADF*	EADF*	Total	Time spent grooming (s)	% hair loss at end of observation
adult/m	4 March	0.02	0	0	0	0	0	0	1	0
calf/f	5 March	0.02	0	0	0	0	0	0	1	2
adult/f	12 March	0.02	0	0	1	4	0	5	1	0
calf/f	12 March	0.05	0	0	0	0	0	0	2	2
adult/m	19 March	44.4	32	148	108	103	0	391	1315	9
adult/m	23 March	0.38	0	0	0	0	0	0	71	17
adult/m	23 March	0.28	0	1	0	0	0	1	266	22
adult/f	26 March	0.32	0	0	1	0	0	1	1	9
calf/m	26 March	0.07	0	0	0	0	0	0	63	1
adult/f	30 March	0.01	0	0	0	0	0	0	40	6
calf/m	30 March	3.27	0	4	3	1	4	12	2072	17
adult/m	30 March	0.87	0	0	1	2	0	3	299	20
adult/m	30 March	0	0	0	0	0	0	0	47	6
adult/f	2 April	0.95	0	0	0	0	4	4	121	20
calf/m	6 April	0	0	0	0	0	0	0	1874	28
calf/m	6 April	0	0	0	0	0	0	0	747	52
adult/m	16 April	0	0	0	0	0	0	0	95	45
	Total	50.7	32	153	114	110	8	417	7016	

* UN = unengorged nymph; EN = engorged nymph; ADM = adult male; ADF = adult female; EADF = engorged adult female.

Eight engorged female ticks were recovered from two samples of dislodged hair. Since I could not be certain whether these ticks were removed by grooming or simply disengaged from the moose because they were fully engorged with blood, I excluded them from the analyses. A significant correlation ($r_s = 0.615$, $p = 0.005$, $N = 17$) was found between weight of hair and numbers of ticks dislodged by grooming. Associations between time spent grooming and (1) dislodged ticks and (2) dislodged hair were low and not statistically significant.

Hair Damage and Loss

There were few differences in prevalence or extent of tick - induced hair damage or loss between Years I and II (Table 2-3). Minor hair damage or loss on moose was first observed in January, 1995 (Year I) and February, 1996 (Year II). That loss initially occurred on the shoulder, neck and withers. Hair damage and loss later expanded to include the rump, perianal region, legs and flanks. By April, hair loss on some moose further expanded to include the back, chest and ears. Individual variation in percent hair on torso that was damaged or lost to grooming ranged from as little as 0.02% - 52%. Mean damage to grooming was about 20% of the lateral torso in April of both years (Table 2-3).

Percent moose with hair damage or loss increased sharply between March and April in Year I and February and March in Year II. By winter's end (April),

Table 2-3. Mean prevalence and progression of winter tick - induced damage and loss to hair coats of moose from Elk Island National Park, September - April, 1994 - 1995 and 1995 -1996.

	No. moose observed			No. (%) moose that groomed			No. moose with hair damage			% moose with with hair damage			Mean % (± SD) hair damage		
	Yr 1	Yr 2	Total	Yr 1	Yr 2	Total	Yr 1	Yr 2	Total	Yr1	Yr 2	Total	Yr 1	Yr 2	Total
September	73	51	124	16(22)	18(35)	34(27)	0	0	0	0	0	0	0	0	0
October	47	42	89	7(15)	6(14)	13(15)	0	0	0	0	0	0	0	0	0
November	33	32	65	6 (18)	6(19)	12(18)	0	0	0	0	0	0	0	0	0
December	41	30	71	11(27)	7(23)	18(25)	0	0	0	0	0	0	0	0	0
January	24	19	43	8 (33)	1 (5)	9 (21)	4	0	4	17	0	9	3 (1)	0	3(1)
February	25	57	82	7(28)	10(18)	17(21)	7	4	11	28	7	13	6 (13)	6(3)	6(3)
March	50	38	88	26(52)	18(47)	44(50)	18	22	40	36	58	45	8 (7)	8(9)	8(8)
April	19	39	58	14(74)	26(67)	40(69)	16	30	46	84	77	79	22(15)	20(12)	20(13)
Total	312	308	620	95(30)	92(30)	187(30)	45	56	101	14	18	16	10(8)	11(7)	9(7)

percent moose with damaged hair coat and mean percent hair damage or loss were similar for both years. On average, 79% of moose emerged from winter (see data for April, Table 2-3) with D. albipictus - induced damage to the winter hair coat.

DISCUSSION

Except for ear twitches, grooming behaviours seen here have been described before for captive and wild moose (Samuel 1991; Mooring and Samuel 1998a, 1999). Some of these behaviours have been described by Geist (1963) as 'comfort movements'. Indeed, the term is appropriate for the time of his study, May - September, which, except for September, is when moose are free of winter tick infestation. Geist (1963) reports 'shaking ' as a rare event, occuring mostly when moose rise from a bed. He saw it 40 times during 237h of observation in May - June; none was observed in July and August during 150h of observation. The fact that shaking was the most frequently observed behaviour in the present study, seen 206 times in 768h of observation and most commonly during March and April when adult ticks are feeding on moose blood, suggest that this behaviour is tick - related. Shaking was a comfort behaviour in the sense that it was used after moose would rise from a bed or be exposed to water (Geist 1963). Shaking was defensive behaviour in the sense that moose used it during peak time of irritation from winter ticks and at the end of other grooming behaviours presumably to remove broken or damaged hair.

Ear twitching behaviour by EINP moose in February and March is likely a result of irritation from ticks bites. It certainly does not coincide with insect activity associated with warmer temperatures of late summer - early fall and spring when biting flies such as members of the Muscidae, Tabanidae, Simuliidae and Culicidae, often pester moose (see Lankester and Samuel 1997). Winter ticks are common on the ears of moose. Berg (1975) found up to 200 engorged winter ticks on the ears of several moose. Samuel and Barker (1979) estimated the density of ticks on the ears of a calf at 3.83 adult ticks/cm^2. In the present study many (specific number unknown) engorged female and male ticks were on both ears of control moose 151.155 (Chapter 3) when she died in April.

However, much like shaking, ear twitching behaviour is probably of little functional significance in removing embedded ticks or providing much relief from tick bites.

Many similarities in grooming behaviour and grooming - related hair loss and damage were apparent between naturally tick - infested moose in EINP and experimentally tick - infested tame moose. As already noted, grooming behaviours of wild moose are the same as those described for captive moose (Samuel 1991). March and April were peak months for increased grooming activity and extent of hair damage and loss for wild and captive moose (McLaughlin and Addison 1986; Samuel et al. 1986; Glines and Samuel 1989; Samuel 1991; Welch et al. 1991). The pattern of progressive hair damage and loss in captive (McLaughlin and Addison 1986; Samuel et al. 1986; Glines and Samuel

1989) and wild moose were the same, although initiation of hair damage and loss may differ somewhat from study to study (e. g., December, Glines and Samuel 1989; January, Samuel et al. 1986; February, McLaughlin and Addison 1986). Hair damage and loss starts on the side of the neck and progresses in a predictable fashion; i. e., outward from the neck to about mid - back and downward from the side of neck to the top of the leg, forming the characteristic triangular - shaped area of hair damage and loss (as viewed on the lateral torso).

Despite these similarities, differences in grooming between free - ranging, naturally tick - infested moose from EINP (present study) and captive, experimentally tick- infested and unifested, tame moose (Samuel 1991) were notable from a number of comparative perspectives. The predominate grooming behaviours for captive moose were licking and rubbing, followed by scratching and shaking (Samuel 1991), whereas, those of free - ranging moose were shaking and licking followed by rubbing and scratching. However, shaking was used more by uninfested, then by infested, captive moose, and mostly during May when moose were shedding the winter hair coat (Samuel, et al. 1986).

Moose at EINP groomed 1.3% (± 0.8) of the total observation time, September - April, while infested and uninfested captive moose groomed 5.6% and 0.3%, respectively, late October - June (Samuel 1991). Elk Island moose had fewer events/h of grooming and invested less time (duration) grooming in all months compared to infested tame moose (Table 2-4). Except for March and April, wild moose groomed less also than captive control moose (Table 2-4).

Table 2-4. Comparison of approximate mean monthly grooming frequencies (events/h) and duration (s/h) for captive, experimentally - infested and uninfested tame moose (Samuel 1991)* and free - ranging, naturally - infested wild moose in Elk Island National Park (present study).

	Captive * **		Free - ranging
	infested	uninfested	infested
Frequency:			
Sep	-	-	2.0
Oct	7.7	0	0.5
Nov	4.8	0.8	0.5
Dec	8.4	0	0.6
Jan	10.1	1.2	1.0
Feb	16.0	2.3	1.3
Mar	23.5	0.7	2.5
Apr	19.1	1.3	5.8
Totals	89.6	6.3	14.2
Duration:			
Sep	-	-	134.4
Oct	74.9	0	32.0
Nov	66.3	19.0	49.3
Dec	64.9	0	25.0
Jan	155.2	7.1	22.0
Feb	200.9	11.1	97.5
Mar	336.1	4.6	46.0
Apr	245.8	15.2	268.8
Totals	1144.1	57.0	675.0

* * 13 moose infested with 30,000 or 50,000 tick larvae and 11 moose uninfested.

Why is it that moose in EINP, which host many ticks annually, groom less than captive moose with similar average numbers of ticks? There are no sure answers, but differences might merely reflect the differences between a captive and free - living life style for moose. Captive moose, constrained to pens and provided a highly nutritious and ample supply of food, do not have to perform some of the daily activities necessary for survival in the wild. These include food acquisition and vigilance against predators. Furthermore, captive moose received as neonate calves and raised by 'human parents', are usually well habituated to man and the conditions of captivity. In all probability they are not under a lot of stress and because their energy expenditure is, therefore, minimal, have both the time and energy to devote to grooming.

In contrast, wild moose are subjected to variations in quality and quantity of food and the vagaries of winter weather, such as prolonged periods of intense cold temperatures, severe wind chill or deep crusted snow affecting mobility and food searching efforts. Considering that moose spend most of their time (roughly 98%), hence energy, in winter searching for food, eating and ruminating (Risenhoover 1986, 1987; Renecker and Hudson 1989; Gillingham and Klein 1992), and that winter diets generally do not supply enough energy to meet daily maintenance requirements (Regelin et al. 1985; Renecker and Hudson 1986), wild moose might simply lack the time and/or energy to do much grooming.

Samuel (1991) discussed the relative lack of tick - induced alopecia on the moose of EINP compared with a moose population 150km north of EINP, and suggested that host nutrition was involved. He rationalized that the immune responsiveness of moose may be compromised because of the relatively poor condition of the range due to overbrowsing by high numbers of ungulates in the Park. Thus, as a consequence of poor nutrition, moose in the Park groom less, have minimal hair loss, carry more ticks and suffer more loss of blood.

While the apparent overbrowsed condition of the Park was suspect when Samuel (1991) proposed his scenario for EINP moose, the 15 - 20% yearly recruitment of moose in the Park seen in the 1980s should negate Samuel's argument in respect to poor quality range (N. Cool pers. comm.). Furthermore, the crude protein (CP) content of winter browse in the Park was between 5.6 - 8.3 % (Cool 1992), which is consistent with CP values, 5.8 - 8.3%, reported for woody twigs consumed by moose in Alberta (Renecker and Hudson 1988) and other areas in North America (Oldemeyer et al. 1977; Crete and Jordan 1982; Risenhoover 1987). Because protein serves as a source of energy and provides amino acids synthesized by rumen microbes to digest complex carbohydrates (starches, cellulose, hemicellulose and lignin) sugar and fats, the minimum crude protein (CP) requirement for domestic cattle is around 6 - 8% (ARC 1980). Similarly, moose require a minimum dietary CP content of 6.8% to meet maintenance needs (Schwartz et al. 1987).

One factor affecting the nutritional status of moose in EINP that might explain the pattern of little grooming is that of resource competition between elk and moose. Grazing dynamics of the Park's principle ungulates, bison, moose and elk are very complex. Bison and moose feed strictly on grasses and browse, respectively. On the other hand, elk exploit both grasses and browse and, thus, overlap niches of bison and moose. Although interspecific competition occurs between these animals (Blyth 1995) resource partitioning helps ameliorate direct competition (Cairns and Telfer 1980; Telfer and Cairns 1986). Differences in snow depth tolerances between moose, elk and bison probably minimize direct competition for winter resources. Yearly slaughters and live - trapping of these sympatric ungulates, conducted as a preventive measure, also helped them coexist in a fenced Park at fairly high densities.

However, since 1985, when population harvest were reduced for elk and eliminated for moose, the numbers of elk in the Park has increased dramatically from 600 to 2000 elk (Ecosystem Status Report 1994, Norm Cool pers. comm.) Concomitantly, moose productivity declined and since 1991 numbers of moose in the Park have stabilized at about 400 (Ecosystems Status Report 1994). Increased competition from elk for a diminishing browse resource is considered responsible for changes in moose population dynamics (Ecosystem Status Report 1994).

There is some recent, although limited, physiological evidence of severe winter nutritional stress in the Park's moose population. Urine metabolites ratios for winters 1992 - 1993, 1993 - 1994 (Ecosystem Status Report 1994) 1994 - 1995 and 1995 - 1996 (Chapter 3) indicate that the moose population was stressed overwinter. In particular, high U:C ratios, accompanied by elevated C:C ratios, revealed that by late February many moose had limited or no fat reserves (Ecosystems Status Report 1994; Chapter 3). Conversely, elk during that same period were not nutritionally stressed (Ecosystems Status Report 1994; EINP, unpubl.). This suggests that elk had adequate forage resources going into winter or that winter was uneventful in terms of reproductive fitness. Although this evidence is not conclusive, and other explanations not withstanding, competition from elk might result in moose consuming less food during winter, which ultimately would result in moose having less metabolised energy (energy actually used by body tissues) to fuel metabolic process including those of the immune system.

Whatever the mechanism, as a result of reduced grooming, moose at EINP lose less hair by winter's end than do moose from nearby Rochester, Alberta area (Samuel and Welch 1991). From 1979 - 1990 (Samuel and Welch 1991) and 1995 - 1996 (Skorupka, present study), moose in EINP emerged from winter with about 20% of their lateral torso hair coat damaged by tick - induced grooming (Table 2-5). In contrast, tick - induced grooming damage of winter hair for moose from Rochester, Alberta was much higher; mean percent hair coat damage exceeded 40% of lateral torso 8 of 13 winters (Samuel and Welch 1991).

Reasons why moose in EINP groom little in comparison with at least one other moose population nearby are not known. What is needed to help answer the question is research to determine the role nutrition plays in the grooming responsiveness of moose, not only from EINP, but moose from other areas as

Table 2-5. Mean percent winter tick - induced damage and alopecia to lateral torso hair coats of moose from Elk Island National Park and Rochester, Alberta, 1979 - 1990. Data from 1978 - 1990 are from Samuel and Welch (1991) and are based on helicopter or ground surveys conducted between 15 April and 7 May. Data from 1995 -1996 are from the present study and were based on ground surveys during April.

	Mean % hair loss (± SD)															
Winter:	1977 -78	1978 -79	1979 -80	1980 -81	1981 -82	1982 -83	1983 -84	1984 -85	1985 -86	1986 -87	1987 -88	1988 -89	1989 -90	1990**	1994 -95	1995 -96
E.I.N.P.	20		18	21	24	21	10	24	22	24	36	21	20		20	20
	(15)		(13)	(18)	(14)	(14)	(6)	(11)	(17)	(14)	(25)	(19)	(18)		(15)	(12)
Rochester*	41	48	46	47	65	80	35	32	25	35	68	38	42			

* SD not available for mean percent hair loss for moose from Rochester.

** Hair loss data were not collected during Winters 1990-91 - 1993-94.

well. One could look at nutrition from the perspective of specific nutrients; i. e., vitamins and minerals. Little is known about the requirements of moose for these nutrients. However, it is known that animals that are marginally to acutely deficient in nutrient intake suffer some very specific immune system defects, such as diminished antibody response to antigens (Ullrey 1993).

Because the fence that surrounds the Park in effect creates an island situation in which moose and other ungulates exist in isolation from local populations it might be prudent to compare rates of grooming and resulting hair damage seen in EINP moose with those of moose from other island settings such as Isle Royale National Park, Riding Mountain National Park and Cypress Hills. While the results of such studies will do nothing to answer the basic question of why moose in EINP groom little compared to wild moose in non - island situations, it should determine if grooming and corresponding destruction of the hair coat are the same for moose in similar biogeographic situations and, thus, perhaps provide a shaper focus on the direction of future studies.

There is some compelling evidence that winter ticks may affect time budgets of moose. Captive tick - infested moose spent ~ 1h/d January - February and ~ 2 h/d March - April grooming when nymphs and adult ticks, respectively, were feeding on moose blood (Samuel 1991). Free - ranging tame moose spent ~ 9 min/d grooming while ruminating and ~ 3 min/d while standing in October and January (Renecker and Hudson 1989). Although it was not stated that the tame moose were infested with winter ticks, because they were housed at the Ministik Lake Wildlife Research Station, near Edmonton, it is probably safe to assume that they were infested and that grooming was tick - related. Unfortunately, grooming activity was not reported for March and April. Furthermore, Risenhoover (personal communication to W. M. Samuel, 1985) stated that moose in Isle Royale National Park "spent significant amounts of time grooming ticks during foraging bouts", which "lowered intake rates, reduced movement rates and, therefore, influenced foraging efficiency". Increased grooming by moose in EINP, in the present study and in Mooring and Samuel (1998a, 1999), was negatively associated with feeding activity, suggesting that moose sacrifice feeding time in order to groom.

In spite of the limited data set, results on removal of ticks by moose observed grooming are encouraging. The correlation between numbers of ticks dislodged and amount of hair dislodged enhances the proposed biological significance of grooming by Hart et al. (1992). The fact that one bull observed 19 March with no hair damage or loss at the beginning of the observation period, had damaged or removed ~ 9% of its hair coat during 22min of grooming is astonishing. That, combined with the recovery of 391 ticks at the grooming site, and the notation that every bout of grooming resulted in a patch of hair left on the snow, shows how destructive grooming is to the hair coat and, thus, illustrates the cost - benefits of grooming. To further illustrate this point, consider that, at this rate of grooming, by the end of April; i. e., 42d later, this moose could conceivably have removed 89, 721 ticks (based on the estimated mean of 2h/d of grooming cited above for captive moose). This rough estimate is reasonable considering that over a 12yr period, 10% and 20% of moose in EINP were infested with > 80,000 and 50,000 ticks, respectively (Samuel and Welch 1991).

However, as grooming efficiency increases (measured by percent hair loss and number of ticks dislodged) during March and April, fewer ticks should be removed. For example, a calf observed on 30 March with 17% hair loss groomed 34min and dislodged only 12 ticks (Table 2-2). Based on its rate of tick removal (0.35ticks/min x 2h/d x 31 d) an estimated 1, 302 ticks would have been dislodged by 30 April. By comparison a calf observed on 6 April with 28% hair loss did not dislodge any ticks during 31min of grooming (Table 2-2).

The range of ticks removed by grooming for moose in this study, from no hair loss with lots of ticks removed to lesser numbers of ticks removed with increasing hair loss, illustrates the selective force behind grooming; i. e., the removal of ticks. Furthermore, grooming efficiency may point to why moose in EINP have less annual percent hair loss than moose in Rochester (Table 2-5). EINP moose may be less efficient at removing ticks because, as previously discussed, they have less energy to groom than do Rochester moose. Nearly equal numbers of winter ticks are recovered from both EINP and Rochester moose, means of 37,070 and 31,933 ticks, respectively (Samuel and Welch 1991), but hair loss for Rochester moose is twice that of EINP moose (Table 2-5).

What is needed is an experiment involving captive moose with known numbers of ticks to best evaluate the efficiency of grooming in tick removal. Because snow was such a limiting factor in the number of samples collected, I would advise against depending on the presence of snow to collect dislodged hair and ticks. Additionally, captive moose from EINP and Rochester could be used to compare possible intraspecific differences in grooming efficiency.

Mean annual hair loss in a moose population appears to correspond roughly with mean annual numbers of ticks on moose for the same year (Samuel and Welch 1991) (Figure 2-7). For example, when tick numbers on moose in EINP dropped from 65,000 (± 35,000 SD) ticks/moose in winter 1981 - 82 to 12,000 (± 4,000 SD) ticks/moose by winter 1983 - 84, mean percent hair damage dropped also from 24% (± 14 SD) to 10% (± 6 SD). When tick numbers then rose to 48,000 (± 36,000 SD) ticks/moose by winter 1987 - 88, mean hair damage increased to 36% (± 25 SD). From 1988 to 1990 tick numbers declined to 21,000 (± 13,000 SD) ticks/moose and percent hair damage decreased to 20% (± 18). That hair loss should correlate with tick numbers that same winter seems logical based on current knowledge cited above and McLaughlin and Addison (1986). Intuitively, the more ticks feeding on moose blood, the greater the grooming response and the more a moose grooms, the greater the hair loss. This hypothesis was supported by a significant correlation ($\underline{r}_s = 0.76$, $\underline{p} < 0.005$, N =12) between mean annual percent hair loss and mean annual tick numbers on moose.

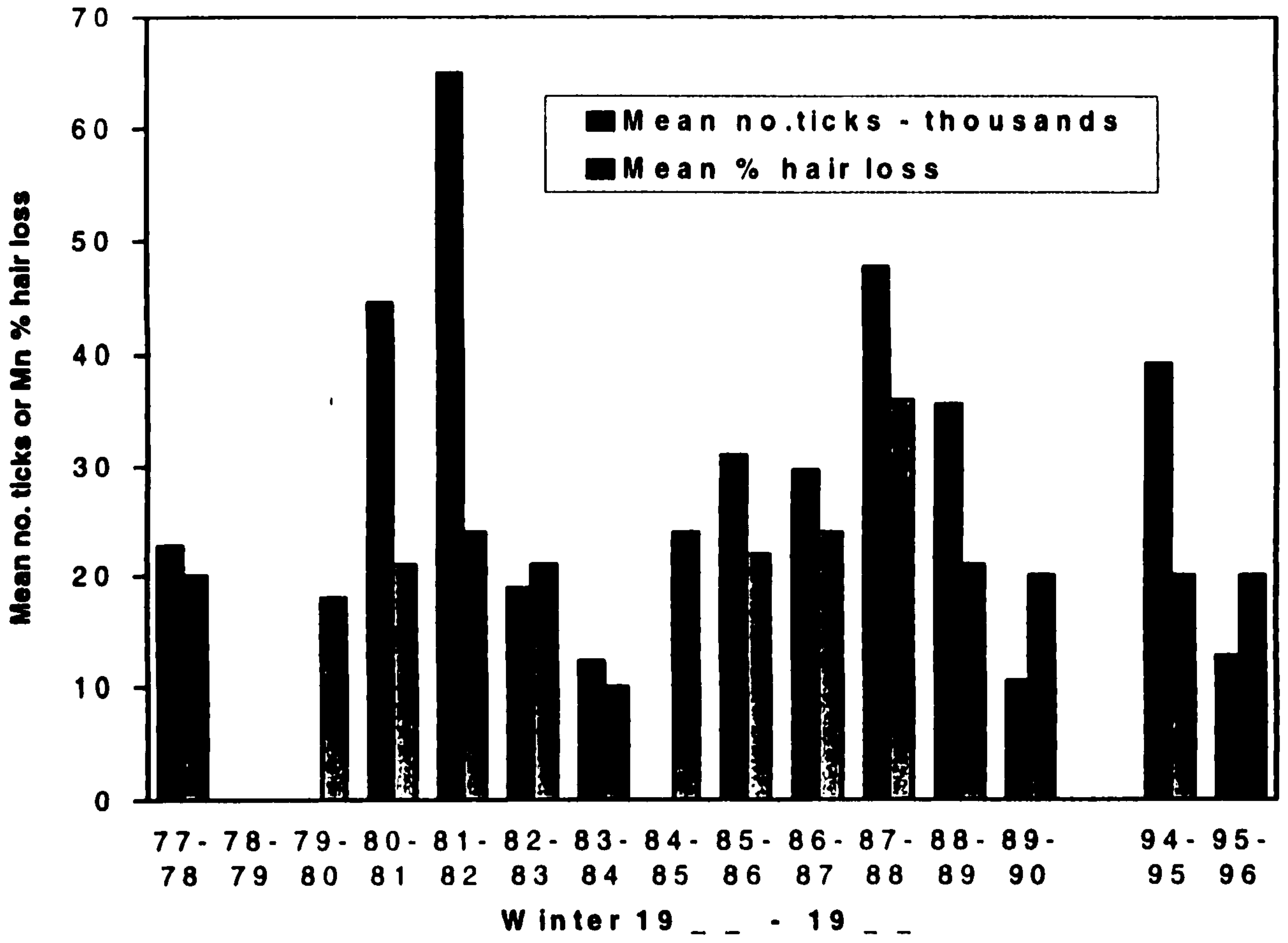

Figure 2-7. Mean annual hair loss and mean annual numbers of ticks on moose from Elk Island National Park during winters 1977 - 1978 through 1995 - 1996. Data from winters 1977 - 1978 through 1989 -1990 are from Samuel, unpublished.

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CHAPTER 3

Effects of winter ticks (Dermacentor albipictus) on aspects of behaviour and nutrition of free - ranging moose (Alces alces) in Elk Island National Park, Alberta

INTRODUCTION

Winter ticks (Dermacentor albipictus) are assumed to be a significant fitness cost for moose. This is because winter tick infestations, at least on captive moose, are associated with weight loss, anaemia and other physiologic effects (Glines and Samuel 1989), depletion of visceral fat reserves (McLaughlin and Addision 1986), reduced mass gains (Addison et al. 1994), restlessness and extensive grooming (Samuel 1991) and severe damage to the winter hair coat (McLaughlin and Addison 1986; Samuel et al. 1986; Glines and Samuel 1989; Welch et al. 1990). It is thought that extensive tick - induced alopecia, depletion of fat reserves and anaemia may result in thermal stress and greater metabolic demands, and in severe cold, hypothermia (Samuel 1991). Although hair damage and alopecia on tick - infested moose are rarely extensive before March (Glines and Samuel 1984; Welch et al. 1990; Samuel and Welch 1991; Mooring and Samuel 1999) and, at normal late winter temperatures, moose can compensate for loss of insulation by restricting respiratory heat loss (Welch et al. 1990), it is quite possible that the effects of ticks on moose in times of stress, such as that produced by long winters, could be quite severe (Samuel 1991; DelGiudice et al. 1997).

Samuel (1991) noted that the intense 'itch' associated with feeding ticks appears to interrupt the daily activities of captive moose in that they spend less time lying down than tick - free moose. There are no similar reports for wild moose, but Risenhoover (1987) reported that tick - infested moose in Isle Royal National Park (ISRO), Michigan, spent 4h/d resting and 11h/d ruminating while tick - free wild moose in Denali National Park and Preserve (DNPP), Alaska, spent 6h/d resting and 12h/d ruminating. Furthermore, Rishenhoover (1987) noted that during foraging periods ISRO moose spent an unspecified amount of time engaged in non - foraging activities; specifically 'grooming', presumably in response to winter ticks. Similarly, increased grooming by tick - infested moose in Elk Island National Park was negatively associated with feeding activity, suggesting that moose sacrifice feeding time in order to remove engorging ticks (Chapter 2 and Mooring and Samuel 1999).

Glines and Samuel (1989) speculated that fatigue associated with tick - induced anaemia may prevent moose from travelling necessary distances to find suitable forage. Even if moose find suitable areas in which to forage, lethargic moose may feed indiscriminately on whatever browse that is close at hand rather than seek out more palatable food. Evidence of such random feeding by a tick - infested moose in late winter was presented by Hatter (1950). Despite the fact that "all key browse species were present in better than average densities" movement was not directed towards selecting such browse, instead the moose foraged on food "as she came to it" (Hatter 1950).

In either case the extent to which winter ticks affect the normal daily activities of wild (free - ranging) moose has not been studied in much detail. Do moose sacrifice feeding time for grooming? Alternately, or perhaps concurrently, does the intense itch and irritation associated with feeding D. albipictus, and the apparent resulting restlessness, affect foraging efficiency? Conversely, would moose feed less selectively if they suffer from tick - induced lethargy?

Winter is an energetically stressful time for moose. In general, food supplies are diminished and can be of such poor quality that they do not meet minimum energy requirements (Schwartz et al. 1987, 1988; Renecker and Hudson 1989a). Energy intake is reduced and, as a consequence, moose enter negative energy balance and lose weight (Schwartz et al. 1988). In order to supplement energy deficits, moose draw upon stored body fat and endogenous protein to help them survive.

Stress plays an important role in starvation in that it mediates the rate at which energy reserves are consumed (Saltz and White 1991; Saltz et al. 1995). During periods of chronic stress, cortisol, a glucocorticoid hormone, is secreted by the adrenal gland into the blood to mobilise energy reserves (Stephens 1980; Burch 1994). Initially, cortisol acts on fat reserves, sparing lean muscle tissue, but as these reserves become depleted catabolism of muscle protein increases (Cahill 1979; DeCalesta et al. 1975; Bahnak et al. 1979; Brodsky 1998). Furthermore, if starvation is accompanied by an additional stressor, such as extreme low temperatures or poor weather conditions, physical injury, or disease, plasma concentrations of cortisol increase (Klasing 1985) and the muscle sparing affect is compromised (Panaretto 1968).

As indicated at the beginning of this chapter, one possible stressor affecting moose is winter ticks. When ticks feed they (1) remove blood and nutrients (Kaufman 1989), (2) introduce toxins and other pharmacologically active substances that cause immune reactions (Brossard et al. 1991), (3) alter blood chemistry (Glines and Samuel 1989) and (4) suppress the appetite (O' Kelly et al. 1971). The time of most stress for moose occurs during mid - to - late winter and early spring, when nymphal and adult tick life - stages are feeding on blood, body reserves of moose are usually low and the need to conserve energy is most likely critical.

In an attempt to better understand how infestations of winter ticks might affect the nutrition of free - ranging moose during winter, I conducted a manipulative field experiment at Elk Island National Park, Alberta, during winter 1994 - 1995 (referred to as Winter I) and 1995 - 1996 (referred to as Winter II). This study was designed to examine how tick - induced grooming affected overall activity budgets, diet quality and body condition of free - ranging moose. Several moose were caught, fitted with radio collars and some were treated for ticks with ivermectin, an anti - parasitic drug. Behavioural observations of treated and untreated control moose were made to determine the effect of tick - induced grooming on activity budgets. Urine deposited in snow was collected from treated and control moose and analysed for urea, creatinine and cortisol to assess body condition. Faeces was collected from moose in both treatment groups and analysed for faecal crude protein and lignin content to assess diet quality. The predictions were that

1. tick - induced grooming by moose interferes with time spent foraging, resting or ruminating;

2. tick - caused irritation or fatigue causes moose to forage less efficiently, and;

3. the stress of winter ticks feeding on moose blood exacerbates the rate of endogenous protein catabolism, thus, affecting body condition.

METHODS

Description of Study Site

The field experiment was done at the Mud Lake ungulate management facility in EINP. (See Chapter 2 for a brief description of EINP, its plants and large mammals). Mud Lake facility is located on the west side of the Parkway and extends north from the south entrance of the Park northward to the northern shore of Mud Lake, then west to the east side of Little Tawayik Lake trail (Figure 3-1). It is enclosed by a 2.2m - high game fence and contains approximately 5km^2 of typical aspen parkland. Within the facility there are six interconnected paddocks, several alleyways and chutes and a series of corrals and holding pens. There are two livestock squeezes, both of which have been modified for use on

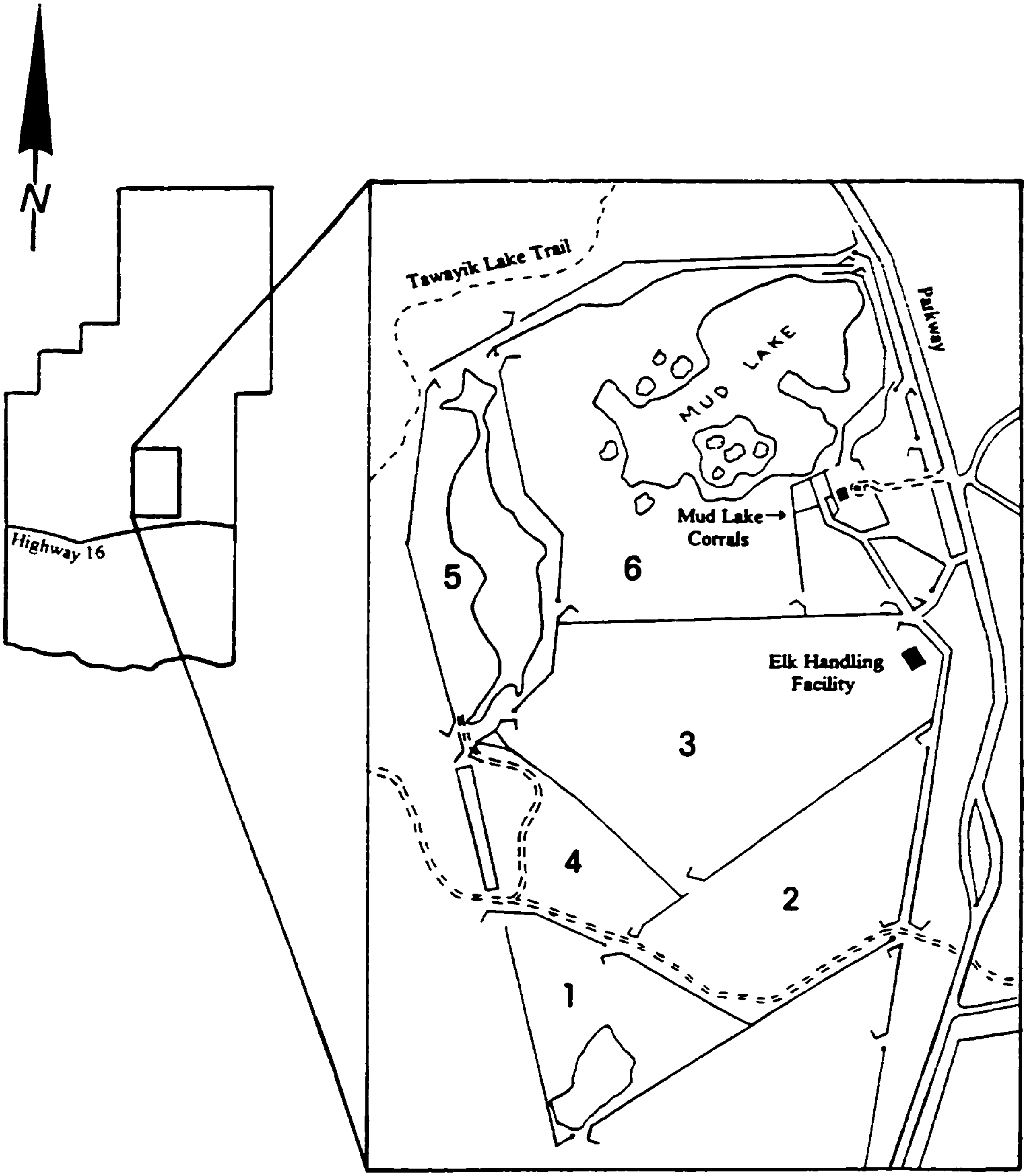

Figure 3-1. Map showing location of Mud Lake ungulate management facility in Elk Island National Park, Alberta, Canada. (Map courtesy of Parks Canada)

large ungulates. One squeeze apparatus is located outdoors adjacent to the Mud Lake corral complex; the other one is inside the elk facility building, which is located in the north-east corner of paddock 3 (Figure 3-1).

Trapping

Eight moose, five adult females and three calves were captured in elk traps located throughout the Park during late November and early December, 1994, and transported by trailer to corrals in the Mud Lake facility (Table 3-1). Elk traps were not used to capture moose during Winter II. Instead the outer gates in enclosures 4, 5, and 6 were opened over summer 1995 to allow moose to enter the facility. In December the gates were closed and six moose, four adult females, one calf and one yearling bull, were trapped and later moved to the elk handling facility. Any elk, deer and bison present in the facility were hazed from the enclosure with the use of snowmobiles.

On December 21, 1994, the eight moose were moved from the Mud Lake corrals, via a system of chutes into the outdoor livestock squeeze apparatus where they were restrained and blindfolded. An attempt was made to keep noise to a minimum while a numerically - coded ear tag was attached to the animal's left ear and either a colour - coded LMRT3 or LMRT4 Lotek electronic radio collar[1] was placed around the animal's neck. Moose in winter I were given

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[1] Lotek Engineering Inc., 15 Pony Drive, Newmarket, Ontario, L3Y 7B5

one 1.72g sustained - released formulation Ivomec® SR bolus[2] to reduce or eliminate winter ticks or a gelatine capsule placebo (Table 3-1). Because the bolus uses an osmotic pump to deliver ivermectin at a steady state rate of 10mg/d over 135d, the need to recapture and treat moose with ivermectin a second time was eliminated. Treatment efficacy was based on one bolus/100-300kg body weight for young cattle. Boluses and capsules were administered using a balling gun designed to deliver the projectile into the animal's esophagus. Each moose was observed to insure they swallowed the bolus or gel capsule. Once swallowed the bolus was of sufficient density to be retained in the rumen for the extended period. Trapping and handling procedures for moose and experimental design for tick research were approved by the Biosciences Animal Care Committee, University of Alberta Animal Use Committee.

The same procedures were used on January 25, 1996, except that moose were hazed into the elk facility complex for handling. Only four of the six moose captured during Winter II, the four adult females, were collared and studied (Table 3-1). The yearling bull escaped from the squeeze apparatus and was released and the calf died in the squeeze apparatus. Treatment moose in Winter II were each given two boluses plus a subcutaneous injection of 8cc of ivermectin because the dosage used for moose in Winter I appeared to be too low to eliminate ticks (Table 3-1). Correspondingly, control moose received 8cc of injectable saline solution and two gelatine capsules. In addition moose in Winter

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[2] Merck Frosst Canada Inc., Kirkland, Quebec

Table 3-1. Dosage of ivermectin and date administered to moose in treated and control groups during Winter I, 1994 - 1995 and Winter II, 1995 - 1996, at Mud Lake ungulate management facility, Elk Island National Park.

			Moose		
Date of treatment	No. moose	No. boluses	Age	Sex	No.
December 21, 1994	8	1			
		Treated Moose	Ad	F	151.194[a]
			Ad	F	150.451[a]
			Ad	F	151.175[b]
			Calf	M	151.214[c]
		Control Moose	Ad	F	151.155[d]
			Ad	F	151.186[e]
			Ylg	F	100.001[f]
			Calf	F	151.166[g]
			Calf	F	150.288[f]
January 25, 1996	4	2			
		Treated Moose	Ad	F	y175[h]
			Ad	F	r194[i]
			Ad	F	w186[j]
		Control Moose	Ad	F	r/s155[k]

[a] survived Jan. - Apr., 1995 sampling period.

[b] escaped Mar. 3, 1995, found dead Apr. 27, 1995; observed before & after escaping (see Table 2).

[c] died Feb. 13, 1995.

[d] died Apr. 13, 1995.

[e] escaped Mar. 13, 1995; found dead May 5, 1995; observed before & after escaping (see Table 2).

[f] Calf 150.288 died on Jan. 19, 1995. She was replaced by 100.001, a readily identifiable yearling cow.

[g] died Feb. 27, 1995.

[h] survived Feb. - Apr. 1996 sampling period.

[i] died Apr. 10, 1996.

[j] escaped Feb. 8, 1996, found dead Mar 7, 1996.

[k] escaped Feb. 13, 1996; survived through Apr. 1996 sampling period; observed before and after escaping.

II were given prophylactic intramuscular injection of 10cc penicillin to reduce risk of secondary infection caused by handling procedures. Moose in Winter I did not receive an injection of penicillin.

Data Collection

Grooming Behaviour

Observations of moose were made from January - April, 1995, and February - April, 1996. A Telonics receiver and hand - held antenna were used to locate radio - collared moose each morning and afternoon, 4 - 5 d/wk. Sometimes, 10X binoculars were needed to observe moose in heavy brush or at great distance. Duration of observation was often dictated by the observability of moose, but did not exceed 15min.

Events of grooming behaviours, licking, rubbing, scratching or shaking (Samuel 1991) and activity states were recorded during each focal animal observation period. (See Chapter 2 for descriptions of focal animal sampling, events and activity states.) The duration (in seconds) of all grooming activity/ behaviours during each focal animal observation period was recorded.

Activity states were categorized as foraging, which included all movement associated with searching for and ingesting food; bedded (resting); ruminating (while bedded); standing idle; moving (movement not associated with foraging such as walking or running); alert behaviour (standing or bedded); miscellaneous (drinking water or eating snow, chewing while standing and social interactions); grooming; and pacing. Pacing was a rather unusual behaviour consisting of a combination of walking and standing idle. Moose would walk, then stop walking and stand idle. The brief sequence, which lasted, generally, < 2 - 3min, would then be repeated. Pacing activity would be performed for part, if not all, the sampling period. The cause of this behaviour is not known.

Transition times; i. e., the beginning and end of each activity state and event of grooming, were recorded during each focal animal observation period in the order in which they were observed. This provided information on the time spent in various activities and enabled me to determine behavioural states at 2min intervals. These instantaneous scan samples (Altmann 1974; Martin and Bateson 1993) were later transformed to percent total scans activity (Altmann 1974).

A random numbers table (Zar 1984) was used to assign moose from each treatment group to a daily observation schedule. Each group of moose were observed on alternate days during Winter I. However, all four moose were observed each day during Winter II. Moose observed first in the morning were observed last in the afternoon. This within day rotation was done in consideration of daily changes in temperature and weather conditions that might affect behavioural activities of moose.

Because of the loss of animals, repeated measures were not possible. Instead, repeated measures of individual moose in both treatment groups were replaced with their respective monthly means. These were then used to calculate the monthly group means.

Behavioural and activity data obtained in January, 1995 from moose 150.288 were combined with data from replacement moose 100.001 (Table 3-1). Monthly mean frequency of grooming (events/h) was calculated using the group mean for all moose that were observed. Monthly mean duration (s/h) of grooming was determined using the group mean for only moose that groomed.

Attempts were made to locate and observe, as well as collect urine and faecal samples from moose that escaped during Winters I and II. (Appendix 1). Most attempts during Winter I were successful. However, few behavioural (grooming and activity) and urine data were collected from control moose r/s 155 during Winter II. Because of this, comparisons with treated moose that same year were not possible. Instead, mean annual tick infestations from treated moose in Winter II were compared with those from treated moose in Winter I in an attempt to evaluate the efficacy of ivermectin dosages on tick infestations.

Winter Ticks on Moose

Half - hides (i. e., right or left lateral half, depending on which side was up when moose died) were collected from an untreated calf (151.166) and cow (151.155) that died during Winter I (Table 3-1) and from a non - study bull, calf and cow that died or were shot by Park Wardens during Winter II to obtain a rough estimate of annual tick infestations on moose. The non - study cow moose hide was provided by M. Mooring. A total of four half - hides were collected from treated moose (Table 3-1). Two came from calf 151.214 and cow 151.175 during Winter I and two from cows w186 and r194 during Winter II. Hides were digested following the techniques described by Welch and Samuel (1989). Briefly, each half - hide was marked into a 10 X 10 cm square grid, then sketched on graph paper with each 100 cm^2 square numbered sequentially. Using a table of random numbers (Zar 1984), 15% of the numbered squares were digested in 5% potassium hydroxide solution with a small amount of liquid dish detergent added. Winter ticks from the digesta were transferred to white enamel pans and counted. The estimated total number of ticks (and densities) on a full hide were extrapolated from the 15% sample.

Hair Damage and Loss

In order to assess hair damage and loss caused by grooming, the extent of hair damage and loss were drawn on a moose silhouette diagram. Areas of hair damage and loss data were later converted to percentage surface area of the lateral torso of moose using a digitizing program, Sigma Scan Summa Sketch Plus. Usually only one side was drawn, but if both sides of a moose were drawn, the mean percent surface area was calculated. Winter tick is the only known cause of the characteristic pattern of premature, sequential damage to, or loss of, winter hair on moose (Samuel 1989) and in EINP is the only known ectoparasite on moose (Samuel, personal observation).

Urine and Faecal Samples

Urine deposited in snow and faeces were collected from each moose approximately every 2wk throughout the study. Most collections were made separate from focal animal observation periods, however, if a moose defecated or urinated while being observed, the specimen was collected. Collections followed techniques of Cool (1992); they were made only when moose were observed defecating and/or urinating. The most concentrated portion of snow urine and a minimum of 30g of faeces were collected with a scoop to avoid contamination by skin contact. After each collection the scope was inserted 2 - 3 times in snow to clean it. Care was taken also to assure ground debris was not collected along with faeces. Each urine and faecal sample was placed in a plastic freezer bag and stored at -20 C° until they were analyzed.

Chemical Analysis

Before thawing at room temperature, each frozen urine sample was placed in a second freezer bag to prevent the possibility of cross contamination from bags that may have been damaged during storage. Once defrosted, the contents of each bag were mixed thoroughly and pipetted into 10ml test - tubes. Test tubes were sealed with parafilm, placed in test tube racks and transported to Dynacare - Kasper Medical Laboratories, Edmonton, Alberta for analysis. Quantitative recovery of urine urea (urease procedure) and creatinine (modified Jaffe procedure) were measured by spectrophotometry (Technicon Dax™).

Cortisol was recovered by chemiluminescence detection (Kodak Amerlyte™). Urine metabolites were compared between treatment groups as creatinine ratios. Creatinine is used in the denominator in ratios with urea and cortisol because it corrects for differences in hydration, body mass and dilution in snow (DelGiudice et al. 1988, 1991) and is not affected by fluctuations in daily urine volume or ambient temperature (Cool 1992). Data are presented as urea to creatinine ratios (U:C) in mmol/L:mmol/L and as cortisol to creatinine (C:C) in nmol/L:mmol/L.

Frozen faeces were removed from freezer bags, placed in lunch - size paper bags and dried to constant weights in a drying oven at 60 C°. Dried samples were sent to the Department of Agricultural, Food and Nutritional Sciences, University of Alberta (1995 faecal samples) and to Norwest Laboratories, Lethbridge, Alberta (1996 faecal samples). Faecal crude protein (FCP) was determined by the Kjeldhl procedure (A. O. A. C. 1965). Neutral detergent (cell - wall), acid detergent fibre and permanganate lignin, cellulose, insoluble ash and silica were determined according to Goering and Van Soest (1970). Percent FCP and percent lignin are expressed in g/100g of faeces on a dry matter basis.

Data Analysis

Because tick populations are typically non - normally distributed on host populations (Petney et al. 1990) comparisons between 1) mean frequency and mean duration of grooming, 2) percent hair loss and 3) urine and faecal indices for moose in treated and control groups were by Mann - Whitney test. Correlation analysis of percent activity scans and grooming (all behaviour types combined and specific grooming behaviours) was by Spearman rank - order correlation. Probabilities of 0.05 were considered significant. Means are reported with standard error (± SE) unless otherwise noted.

RESULTS

Overview and Grooming Behaviour

Treated and untreated control moose were observed 61h during Winter I (Table 3-2). This resulted in 179 and 104 observations on treated and control moose, respectively. An additional eight and four observations were made on treated moose 151.175 and untreated moose 151.186, respectively, after they escaped from the facility (Appendix 1). Mean length of an observation was 11min (± 0.4) (range, 2 - 15min). Except for untreated control moose 150.288 and its replacement moose 100.001, animals in both the treated and untreated control groups groomed. Treated and control moose performed 50 and 52 events of grooming, respectively. Mean number grooming events from January - April for treated and control moose were 0.7 (± 0.1) and 0.8 (± 0.1), respectively. Total time spent grooming by treated and control moose from January - April was 426s (mean number s = 5.6 ± 2.8) and 436s (mean number s = 9.2 ± 4.3), respectively.

Table 3-2. Summary of observations on treated and untreated control moose during Winter I, 1994 -1995 and Winter II, 1995 - 1996, in Mud Lake ungulate management facility, Elk Island National Park.

	Winter I			Winter II		
	Treated	Control	Total	Treated	Control	Total
Number of moose observed	4	4	8	3	1	4
Total hours observations	40	21	61	18	0.63	18.63
Number of moose that groomed	4	3	7	2	1	3
Number of grooming events	50	52	102	16	4	20
Total seconds grooming	414	436	850	64	15	79

Treated moose in Winter II were observed 18h, which resulted in 92 observations (Table 3-2). Mean length of an observation was 11min (± 1) and ranged from 2 - 15min. Moose performed 16 grooming events (mean number = 0.6 ± 0.2) and spent 64 s grooming (mean = 2.1s ± 0.9). Four observations, which amounted to 38min, were made on untreated moose r/s 155. Mean length of an observation was 9min ± 0. 1. This moose performed two events of grooming. Total time spent grooming was 15s.

Tick - induced grooming by moose in both treatment groups was first observed in January and February during Winters I and II, respectively. Shaking and licking were the predominant grooming behaviours followed by rubbing and scratching. None of the Mann - Whitney tests comparing frequency and duration of grooming (all behaviour types combined) between treated and control moose during Winter I were significant. Peak grooming rates (frequency and duration) by moose during Winter I coincided with peak parasitic activity in March, but not April (Figures 3-2 and 3-3). However, when frequency of grooming declined during April for both treatment groups, control moose 151.155 continued to spend time licking. In fact this moose spent 12.6s/h licking compared to 1.7s/h for treated moose (Figure 3-3). In terms of specific grooming behaviours, only duration of shaking was significant (MWU, p = 0.042) between treated and untreated groups.

There were no significant differences in activity budgets between treated and control moose during Winter I. Although moose in both treatment groups

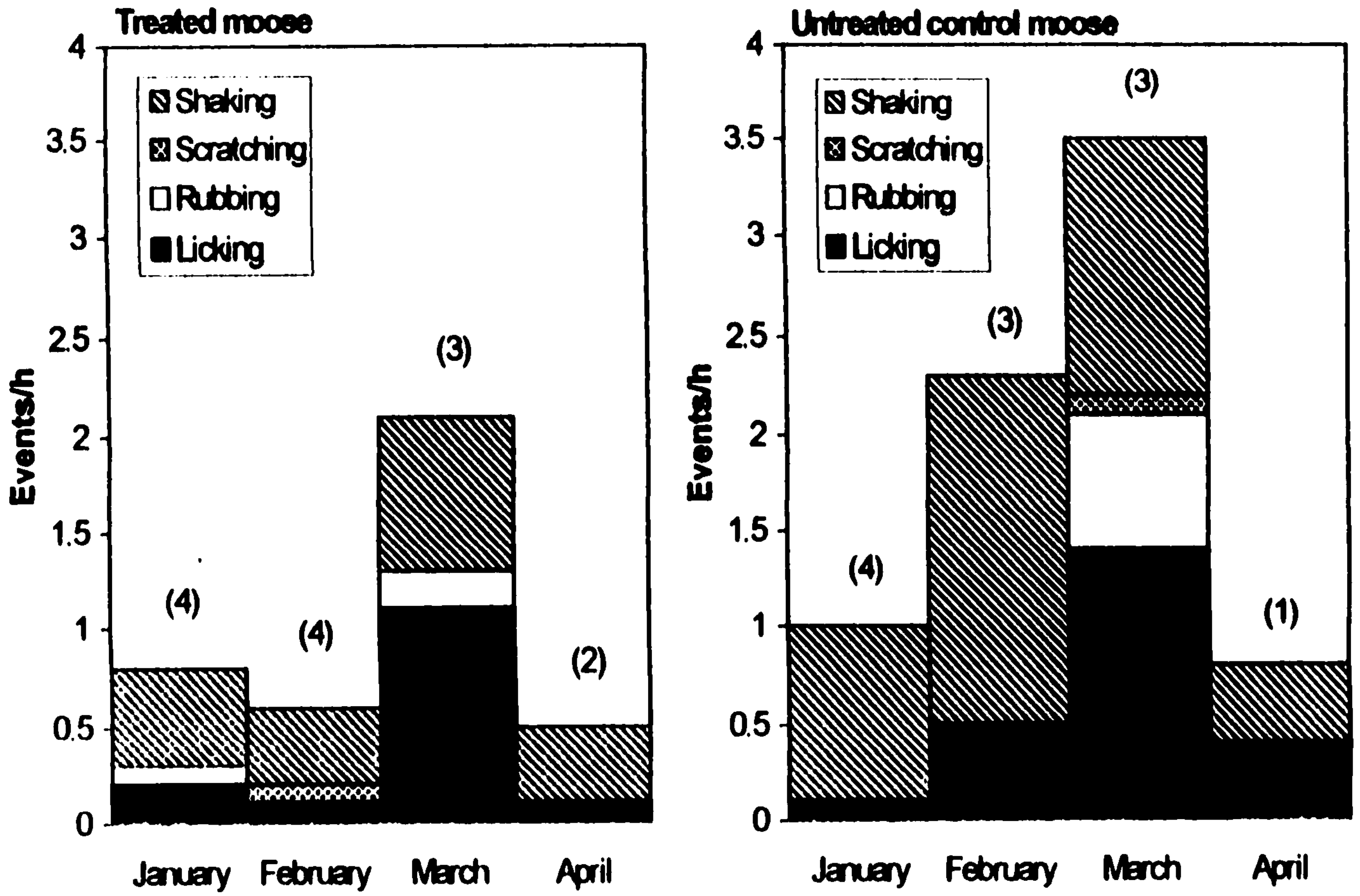


Figure 3-2. Summary of frequency (mean events/h) of grooming activities (behaviours) by treated moose assumed to have reduced numbers of winter ticks and untreated control moose assumed to be infested with winter ticks during Winter I, January - April, 1995, in Mud Lake ungulate management facility, Elk Island National Park.

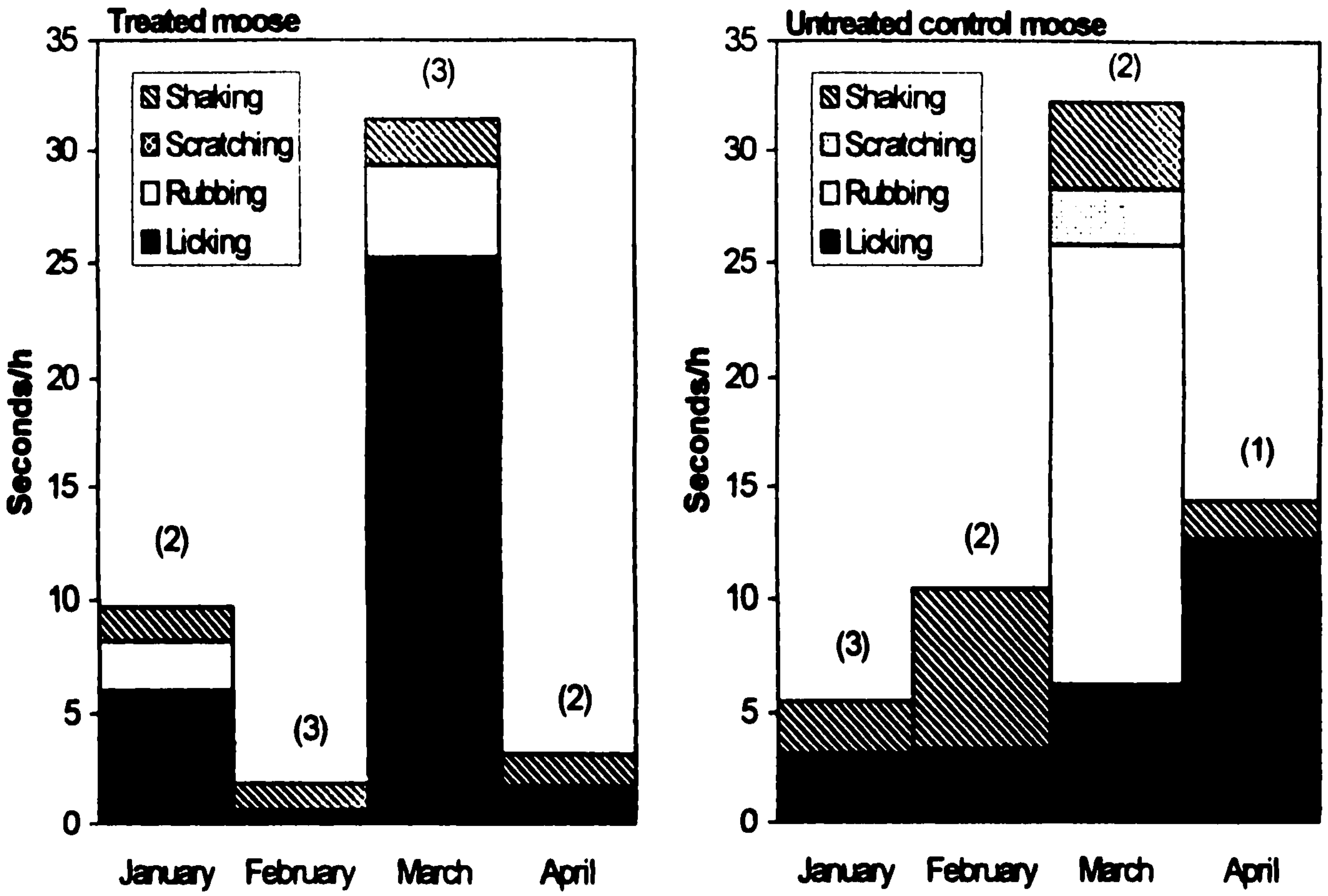


Figure 3-3. Summary of duration (mean s/h) of grooming activities (behaviours) by treated moose assumed to have reduced numbers of winter ticks and untreated control moose assumed to be infested with winter ticks during Winter I, January - April, 1995, in Mud Lake ungulate management facility, Elk Island National Park.

Table 3-3. Mean percent scans activity (± SE) for treated and untreated moose during Winter I, January - April, 1995, in Mud Lake ungulate management facility, Elk Island National Park.

Activity	Treated Moose					Control Moose				
	Jan	Feb	Mar	Apr	Mean	Jan	Feb	Mar	Apr	Mean
	n=4	n=4	n=3	n=2		n=4	n=3	n=2	n=1	
Foraging	41.8	65.5	56.7	41.9	51.4	69.7	42.7	34.0	8.5	38.7
	(8.0)	(12.7)	(12.6)	(10.1)	(5.8)	(12.4)	(8.9)	(0.7)	-	(12.6)
Bedded	14.3	11.8	19.4	20.7	16.6	6.3	25.6	5.7	0	9.4
	(6.3)	(4.3)	(6.6)	(9.0)	(2.1)	(4.3)	(7.3)	(5.7)	-	(5.6)
Ruminating	3.6	0	0	17.8	5.4	0	0	5.7	42.7	12.1
	(3.6)	-	-	(4.1)	(4.2)	-	-	(5.7)	-	(10.3)
Pacing	29.3	16.4	11.7	13.8	17.8	11.4	20.6	26.3	19.5	19.5
	(12.8)	(11.3)	(8.1)	(9.8)	(4.0)	(2.0)	(18.3)	(18.2)	-	(3.1)
Standing	6.2	4.0	5.5	3.9	4.9	4.4	1.0	20.5	22.0	12.0
	(1.0)	(3.2)	(2.1)	(3.9)	(0.6)	(2.1)	(1.0)	(3.8)	-	(5.4)
Moving	2.9	0.7	2.3	0.3	1.6	0	0.5	1.2	6.1	2.0
	(1.3)	(0.7)	(1.3)	(0.3)	(0.6)	-	(0.5)	(1.2)	-	(1.4)
Alertness	1.0	1.4	0.2	1.1	1.0	6.3	5.3	0	0	2.9
	(0.6)	(1.4)	(0.2)	(1.1)	(0.3)	(3.6)	(3.6)	-	-	(1.7)
Miscellaneous	0	0	0	0	0	0.3	0	1.6	0	0.5
	-	-	-	-	-	(0.3)	-	(1.6)	-	(0.4)
Grooming	0.3	1.8	4.1	0.6	1.7	0.7	3.8	8.1	1.2	3.5
	(0.3)	(0.5)	(0.4)	(0.0)	(0.9)	(0.7)	(3.0)	(2.5)	-	(1.7)

spent the most time foraging, treated moose spent more time overall in this activity than untreated control animals (Table 3-3). This was particularly noticeable during March and April when percent scans for treated moose was 56.7% and 41.9% compared to 34.0% and 8.5% for untreated moose, respectively. Time spent bedded was higher also for treated moose. In fact, except for February, control animals spent very little time bedded, especially during March and April. The least amount of time was devoted to ruminating by moose in both treatment groups, but during April, time spent in this activity increased, especially for control moose.

Strong negative correlations were found between duration of licking and percent scans foraging for untreated control moose ($r_s = -1.00$) (Figure 3-4) and between percent scans grooming (all behaviour types combined) and percent scans pacing ($r_s = -1.00$) for treated moose (Figure 3-5). Although these relationships were highly correlated, they were significant at $p = 0.10$ only.

Several other strong compensatory but non - significant correlations ($r_s = -8.00$) were noted also for untreated moose. These were between 1) duration of grooming (all behaviour types combined) and percent scans foraging 2) duration of licking and percent scans bedded and 3) frequency and duration of shaking and percent scans standing.

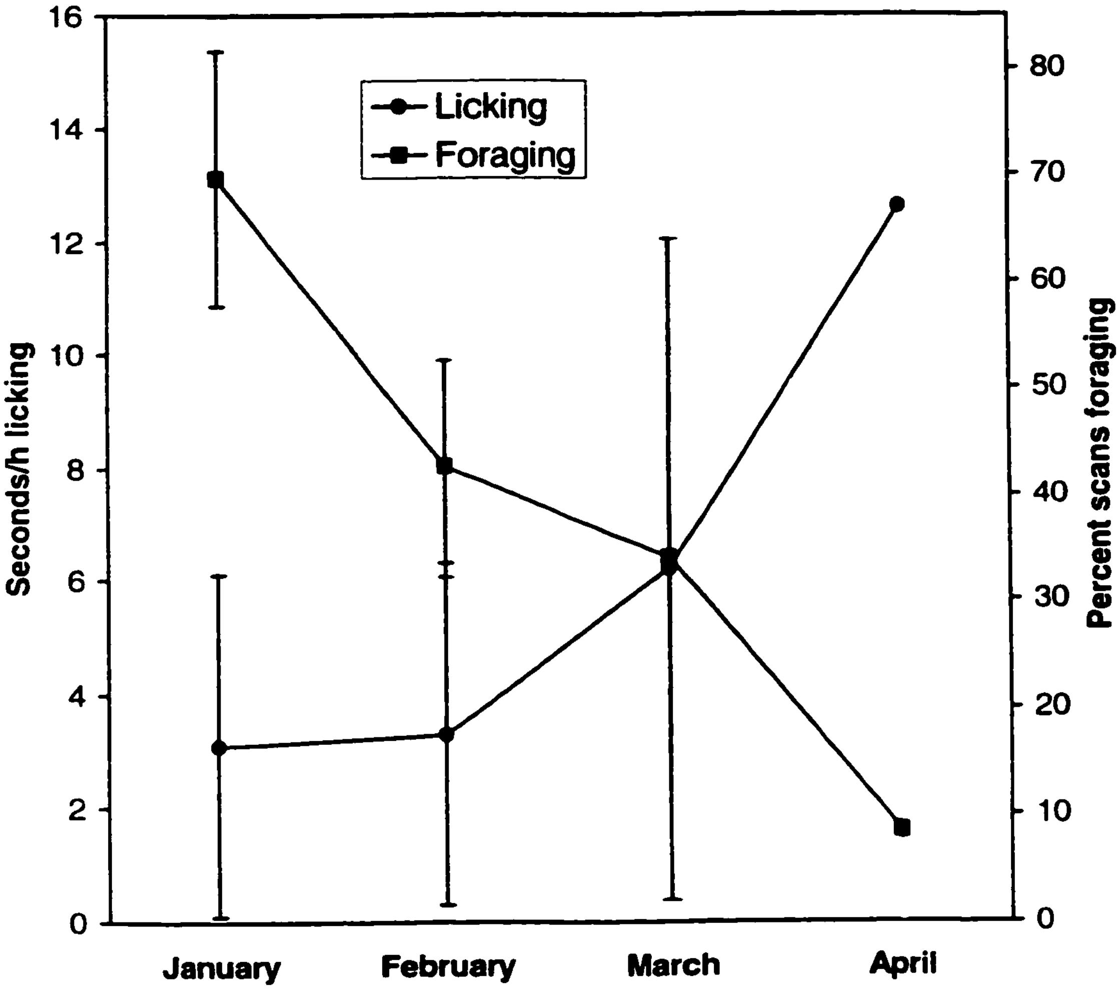


Figure 3-4. Mean percent scans foraging and duration (mean s/h) of licking by untreated moose during Winter I, January - April, 1995, in Mud Lake ungulate management facility, Elk Island National Park. Spearman rank - order correlation = -1.00, p = 0.10. Sample sizes for duration of licking are on Figure 3-3 and sample sizes for percent scans foraging are on Table 3-3.

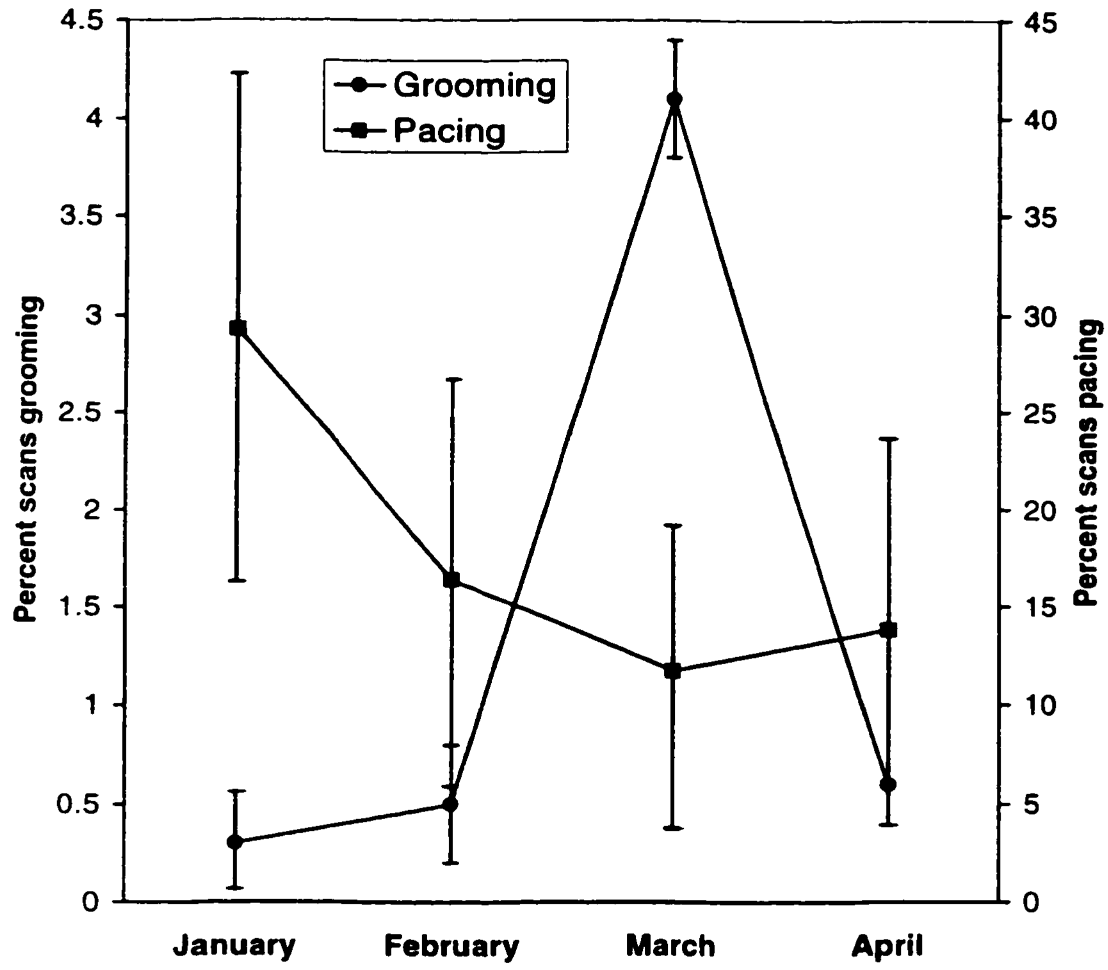


Figure 3-5. Mean percent scans grooming (all behaviour types combined) and mean percent scans pacing by treated moose during Winter I, January - April, 1995, in Mud Lake ungulate management facility, Elk Island National Park. Spearman rank - order correlation = -1.00, p = 0.10. Sample sizes are on Table 3-3.

Table 3-4. Estimated numbers and densities of *Dermacentor albipictus* recovered from hides of untreated and treated moose during Winter I, 1994 - 1995 and Winter II, 1995 - 1996, Elk Island National Park.

	Winter I						Winter II				
	Date collected	Numbers of		Total Ticks	Density (cm^2)		Date collected	Numbers of		Total Ticks	Density (cm^2)
		nymphs	adults					nymphs	adults		
Control moose						Control moose					
calf	27 Feb	38080	20747	58827	4.9	cow	27 Jan	5627	213	5840	0.5
cow	13 Apr	907	18720	19627	1.0	bull	13 Mar	2293	13440	15733	0.7
						calf	19 Mar	7453	9320	16733	1.9
Treated moose						Treated moose					
calf	13 Feb	40333	1973	42306	2.8	cow	7 Mar	6147	1107	7254	0.5
cow	27 Apr	240	8653	8893	0.7	cow	10 Apr	2453	2187	4640	0.3

Winter Ticks on Moose

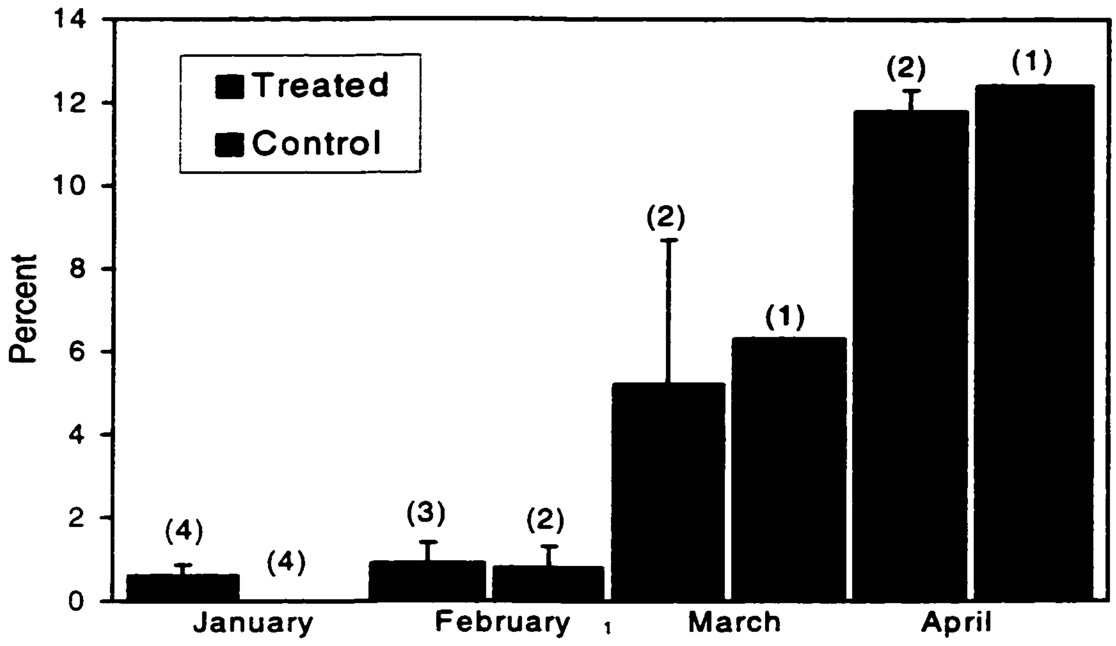
Numbers of ticks and tick densities from several treated and untreated moose during Winters I and II are shown on Table 3-4. Between year differences in tick infestation and in tick densities on treated moose were not significantly different. The same was true for untreated control moose.

Hair Damage and Loss

The extent and progression of hair damage and alopecia were similar for treated and control moose during Winter I (Figure 3-6). At its peak, damage was still only 12% of the lateral torso. The spatial distribution of hair damage on lateral torso was similar to that reported for moose by McLaughlin and Addison (1986) and Samuel et al. (1986). Only one treated moose (y175) had hair damage and loss during Winter II. Damage/loss was minimal and consisted of a few small patches on her shoulder. By comparison, mean percent hair loss for untreated control moose r/s175 was 11.8%. Differences in percent hair loss between treated and control moose during Winter II were significant (MWU, p = 0.053).

Urine Indices

Both U:C and C:C ratios reflected differences in changes in body condition overwinter of control and treated moose (Figure 3-7). However, only U:C ratios between the two groups were significant (MWU, p = 0.050). Overall U:C ratios



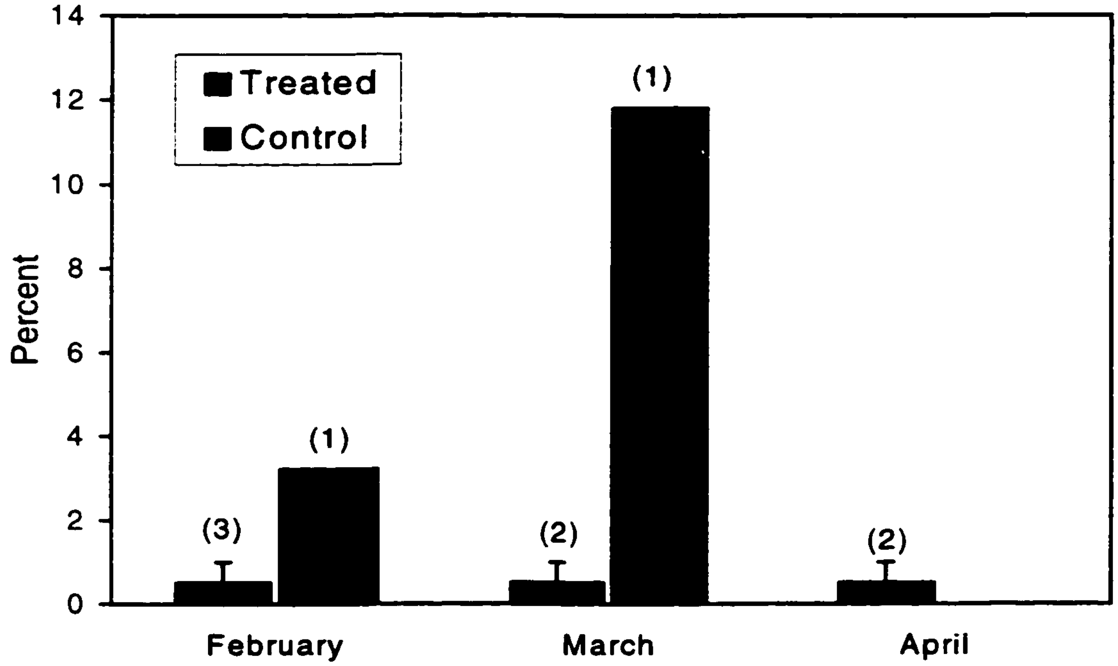


Figure 3-6. Mean percent hair damage and loss (± SE) on lateral torso of treated and control moose during Winter I, January - April, 1995, (top figure) and Winter II, February - April, 1996, (bottom figure) in Mud Lake ungulate management facility, Elk Island National Park .

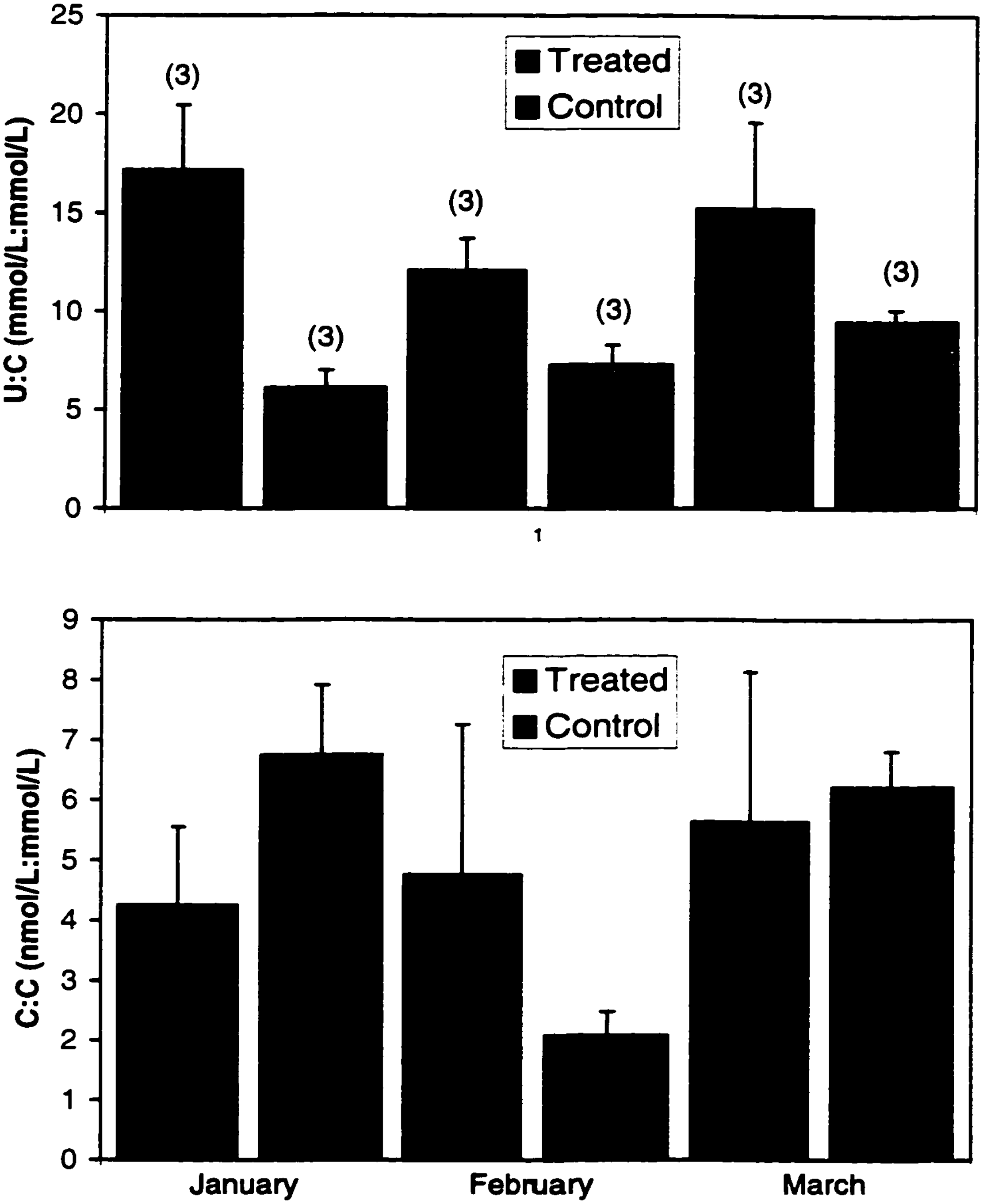


Figure 3-7. Mean (± SE) urea nitrogen : creatinine (U : C) and urea cortisol : creatinine (C : C) voided in snow by treated and control moose during Winter I, January - March, 1995, in Mud Lake ungulate management facility, Elk Island National Park.

were higher for treated moose. C/C ratios for treated moose remained relatively constant during winter, ranging narrowly between 4.2 - 5.6. By comparison C/C ratios for untreated control moose increased from 2.1 in February to 6.2 in March.

Faecal Indices

There were no significant differences in either percent faecal crude protein (FCP) or percent lignin between moose in treated and untreated control groups during winters I and II (Table 3-5). Neither FCP nor lignin values varied much for moose in both treatment groups during Winter I. From January - April FCP ranged from 6.7 - 7.5 for treated moose and from 6.9 - 8.3 for control moose. Lignin values ranged narrowly also from 25.0 - 28.5 and from 26.1 - 28.5 for treated and control moose, respectively. Similar trends in faecal indices were seen during February and March of Winter II between treated and control moose.

DISCUSSION

In spite of many problems associated with moose escaping and dying, and a drug that did not work all that well against ticks at dosages applied, some important patterns emerged from the data set. The finding that time spent grooming by untreated moose was negatively correlated with feeding activity suggests that moose sacrifice feeding time in order to remove engorging winter

Table 3-5. Mean percent faecal crude protein (FCP) and percent lignin (± SE) for treated and untreated control moose during Winter I, January - April, 1995, and Winter II, February - March, 1996, in Mud Lake ungulate management facility, Elk Island National Park.

	Treatment Moose		Control Moose	
	FCP	Lignin	FCP	Lignin
Winter I				
January	7.5 (0.1)	26.9 (1.7)	8.3 (0.2)	26.1 (0.3)
February	7.5 (0.2)	28.5 (0.8)	7.6 (0.3)	26.4 (0.4)
March	6.7 (0.2)	28.5 (0.7)	6.9 (0.2)	28.5 (1.2)
April	7.4 (0.8)	25.0 (2.7)	6.9 -	25.7 -
Mean	7.3 (0.2)	27.2 (0.2)	7.4 (0.3)	26.7 (0.6)
Winter II				
February	6.1 (0.8)	23.5 (0.8)	8.9 -	20.8 -
March	6.5 (0.7)	24.9 (1.0)	6.4 -	26.8 -
Mean	6.3 (0.2)	24.2 (0.7)	7.7 (1.3)	23.8 (3.0)

ticks. This has been reported before (see Chapter 2 and Mooring and Samuel 1999). Potentially, this has important implications for moose. DelGiudice et al. (1997) hypothesized that much of winter tick - imposed stress on moose is attributable to imbalance between nutrient intake and metabolic demands of moose, and that severe 'nutritional restriction' is directly related to preoccupation of infested moose with grooming. Thus, it is possible that tick - induced grooming not only detracts moose from feeding during the critical time of late winter - early spring, but most likely imposed additional energy expenditures on untreated moose. During January the cost of grooming to adult moose over that of bedded - dozing (resting metabolic rate) was 13.1 - 18.7 kJ/(h.kg $^{0.75}$) (Renecker and Hudson 1989b). Unfortunately, these few data are all that are available relative to the cost of grooming by moose. However, it is obvious that the possible effects of winter ticks on energy metabolism of moose warrants further investigation.

Treated moose also increased grooming activity in response to feeding ticks, but did not relinquish foraging time to groom. Instead grooming by treated moose may have taken away from time spent pacing (Figure 3-5). What this implies in terms of nutritional energetics can only be surmised. Renecker and Hudson (1989b) reported that during winter - early spring, energy expenditures of moose while standing were 36% higher than while bedded - dozing (10.8 ± 0.4kJ/(h.kg$^{0.75}$) and from December - January, increments for walking rose steadily from 18.9 - 51.6kJ/(h.kg$^{0.75}$). Based on the relative cost of walking and standing compared to the cost of grooming, it would appear that time spent grooming took away from the apparently more costly activity of pacing and, thus, might have resulted in energy being saved.

U:C and C:C ratios taken together distinguish high dietary protein and energy from that of lean muscle catabolism (Cool 1992). Urinary indices of moose in the present study revealed that endogenous protein catabolism for treated moose was not as pronounced as it was for untreated moose during Winter I (Figure 3-7). The spike in C:C, concomitant with an increase in U:C in March, is indicative of moose losing lean muscle protein at an accelerated rate and implies that untreated moose were leaner; i. e., had less fat reserves. By comparison, U:C and C:C ratios of treated moose suggest that they maintained better body condition overwinter. Furthermore, the gradual increase in C:C ratios from January - March show that treated moose were not excessively stressed in late winter - early spring and that endogenous protein catabolism was not as pronounced for them as it was for untreated control moose.

Faecal indices revealed that treated and untreated control moose consumed diets of similar protein and lignin content during Winters I and II (Table 3-5). Taken at face value these results indicate that winter ticks did not affect foraging efficiency, but as suggested by N. Cool (pers. comm.), moose in the Mud Lake enclosure might not have had much dietary choice.

Lack of food choices might have masked the effects of winter ticks on diet selection. Evidence of this comes from patterns in pacing and standing activities of untreated control moose (Table 3-3), which coincided with major parasitic tick life - stages. (See Chapter 2 for a description of the life - stages of D. albipictus). An important assumption; however, is that pacing activity of moose represents tick - induced irritation and standing idle represents tick - related lethargy. If this assumption proves true then trends in pacing activities showed that untreated control moose were irritated by engorging nymphs during February and by engorging adult ticks during March, and that their initial response to this irritation was to groom. However, during March, standing activities of control moose increased dramatically. One possible reason for this could be that fatigue, associated with tick - caused anaemia, was beginning to affect control moose. Fatigue appeared most pronounced during April when moose 151.155, although likely still highly agitated from engorging female ticks, decreased time spent pacing and grooming in favour of standing idle.

Alternately, pacing activity might be a response to relocation and confinement in Mud Lake facility. However, if this were true, one would expect to see treated moose spending similar amounts of time pacing, but this did not happen. Pacing activity by treated moose was initially high, but decreased overwinter (Table 3-3). Furthermore, the clinical signs of tick - related anaemia; i. e. lethargy, were not evident in these moose. Primary evidence for this is large differences in time spent standing between treated and control moose during March and April, 5.5% and 3.9% compared to 20.5% and 22.0%, respectively.

In order to better evaluate the efficacy of ivermectin it would have been advantageous to know exact numbers of larval ticks infesting moose in the present study. Unfortunately, this was not possible. Instead, winter ticks recovered from hides of untreated control moose provided an estimate of annual tick infestations during Winters I and II, and differences in the number of ticks between treated and untreated control moose that same winter were used as a relative measure of treatment efficacy.

Overall, treated moose during Winter II had 54% fewer ticks than untreated control moose, whereas, treated moose in Winter I had only 35% fewer ticks than untreated controls (Table 3-4). However, the latter estimate might be somewhat inflated because of the relatively low numbers of ticks recovered from the hide of treatment cow 155.175 during Winter I. Reasons for this could be attributed to the time of the year the hide was collected, which was late April approximately one month after peak disengagement of female ticks (Drew and Samuel 1989), or to ivermectin eliminating female ticks during March and April.

Although the efficacy of ivermectin against winter tick infestations on moose is not known, the decision to treat moose with this product was based on results of studies in which ivermectin was shown to be effective against multiple and one - host tick species of cattle, including D. albipictus (Wilkins et al. 1980, 1981; Drummond et al. 1981; Nolan et al. 1981; Lancaster et al. 1982). Because cattle are physiologically similar to moose and because cattle are infested with similar one - host tick species, it was felt that ivermectin would be effective against winter ticks on moose at the same dosage given to cattle. However, results obtained in the present study suggest that the increased dosage of ivermectin administered to moose during Winter II was more effective against winter ticks.

Treated moose in Winter II received a single injection of 8cc ivermectin to bolster the therapeutic effect of the boluses, which required approximately 14d to reach a steady - state rate of delivery. Although the post treatment effect of the subcutaneous injection given to treated moose is not known, its probably safe to assume that ivermectin was effective against ticks during the 2wk interval; i. e., 25 January - 8 February. Single subcutaneous dosages of 100 - 500µg /kg of ivermectin administered to cattle were found to be generally effective against Boophilus microplus, Boophilus decoloratus and Dermacentor albipictus feeding on the day of treatment and for 21d after treatment (Wilkins et al. 1980; Nolan et al. 1981). Because D. albipictus nymphs "dominate the tick population on moose from November to mid - February" (Drew and Samuel 1989), the initial loading dose was likely responsible for the 16% reduction in mean numbers of nymphs on treated moose during Winter II.

Correspondingly, the 6% fewer adult ticks recovered from treated moose during Winter II was likely attributed to the higher combined steady - state rate dosage of 20mg/d delivered by the two boluses. Overall, the combination of treatments resulted in fewer ticks on treated moose during Winter II compared to the single bolus given to moose during Winter I. A combined administration of a single dose of 1.25mg ivermectin and a sustained - released implant of 620mg ivermectin was effective also in eliminating Psoroptes sp. mites in free - ranging bighorn sheep (Ovis canadensis) Boyce et al. (1992).

Interpretation of treatment results obtained for moose in the present study was without benefit of rigorous statistical analysis. Thus, inferences made from this preliminary evaluation are not offered as conclusive proof, but rather suggest that ivermectin reduced numbers of winter ticks on moose. Furthermore, differences in behavioural and physiological indices, some of which were, or approached, statistical significance, appeared to be associated with differences in numbers of ticks infesting treated and untreated control moose. These results implicate winter ticks as impacting nutritional energetics of moose. Under certain environmental conditions, such as long, severe winters, prolonged periods of cold temperatures or high ungulate densities, such as now exist in Elk Island National Park (discussed in Chapter 2), winter ticks may have important biological implications for moose. However, further testing under controlled conditions with larger numbers of animals is required to determine not only the efficacy of ivermectin for moose but also to confirm the preliminary results obtained in the present study.

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CHAPTER 4

DISCUSSION

Animals that live and thrive in environments with fitness compromising ticks evolve behaviours that remove or manage such ticks (Hart 1990). However, for a behaviour to be accepted as having a parasite defense function it must help the host reduce or eliminate the parasite in question and the parasite in question must be detrimental to the host (Hart 1990). Certainly, winter ticks, Dermacentor albipictus, cause problems for moose (Alces alces). They remove blood, causing anemia, alter blood chemistry and deplete visceral fat reserves and perhaps impair liver functions and reduce mass gains (McLaughlin and Addison 1986; Glines and Samuel 1989). Results of urinary indices suggest that the stress of winter ticks feeding on moose blood in March and April increases catabolic activity (Chapter 3). For moose in poor body condition during late winter - early spring, the accelerated loss of muscle tissue might result in death.

Despite the positive correlation between dislodged hair and winter ticks, which indicates that moose remove ticks when they groom, tick - removal grooming by moose appears to be rather inefficient at significantly reducing tick loads (Chapter 2). One reason for this appears to be the pattern of tick - removal grooming. Current knowledge suggests that animals may be motivated to groom by one of two physiological mechanism: an internally regulated program that periodically evokes an event of grooming to remove ticks (and other parasites) before they are able to attach and feed on blood or (2) by the tissue immune system responding to cutaneous irritation from tick bites (Willadsen 1980; Hart et al. 1992; Mooring 1996). Recently, Mooring and Samuel (1998c) provide evidence that grooming behaviour of moose is regulated by the latter mechanism in that moose directed their grooming efforts at removing adult ticks in March and April (Mooring and Samuel 1998c, 1999) rather than the smaller, less costly tick larvae in September and October.

Moose in this study adhered to the stimulus - driven pattern reasonably well in that peak grooming occurred in late winter when nymphs and adult ticks predominate the tick population, rather than in autumn when larvae predominate. However, the secondary grooming peak in September indicates that moose were grooming preventively to remove tick larvae (Chapter 2). But, as stated by Mooring and Samuel (1998c) "It would be naïve to suppose that only one process is involved in the regulation of grooming, and clearly, central - controlled and stimulus - driven mechanisms operate concurrently; in fact, proper functioning of a central mechanism depends upon the stimulus - driven mode for information on current levels of tick infestation." That moose appear to be 'stimulus' groomers is strengthen by the predictions made by the respective models. Thus, the 'programmed' model predicts that hosts grooming the most will have the fewest ticks, because ticks have been removed preventively, while the 'stimulus' model predicts that animals grooming the most will have the most ticks, because they are receiving the most tick - bite stimulation and that they will not groom much when ticks are not feeding (*i. e.*, November, December and January).

Mooring and Samuel (1998c) postulated that the one possible reason for the absence of programmed grooming traits in moose is that the selection pressure favoring evolution of a programmed response has not been operational until recently. Moose are relatively new arrivals to North America (Bubenik 1997) and at some time in the past appear to have acquired not only winter ticks, but also meningeal worm (*Parelaphostrongylus tenuis* and liver fluke (*Fascioloides magna*) from native New World Odocoilene deer (Anderson and Lankester 1974). Holmes (1982) discussed a "class of situations in which parasite - induced mortality in vertebrates appears to be additive and significant - parasites spread from hosts in which they are well adapted to hosts in which they are poorly adapted." That principle appears to apply to these three parasites because all three cause problems for moose but not for deer (reviewed by Lankester and Samuel 1997). Indeed, in regard to winter tick infestation, white - tailed deer appear to adhere to the programmed grooming model. Deer groom most in autumn when tick larvae are attaching to and feeding on deer (Welch et al. 1991).

One significant feature of a parasite becoming a pathogen is that pathogenicity is correlated with high numbers of parasites. Thus, a host with limited co - evolution with a parasite (*e.g.*, winter tick and moose) and environmental factors that increase transmission are likely to increase the likelihood of pathogenicity (Holmes 1996). One thing that can be said for moose is that they hosts lots of winter ticks. Samuel and Welch (1991) recorded a minimum density of at least 1.1 ticks/cm^2 skin surface for 212 moose from British Columbia, Manitoba and Alberta, 1977 - 1990. Minimum densities for moose are still high when compared to mean densities reported for elk, bison and caribou, all of which were ≤ 0.57/cm^2 (Welch et al. 1990b; Mooring and Samuel 1998a, b).

For grooming behaviour to be adaptive it must not only maintain low tick numbers, but it must also balance the cost of grooming against the cost of being parasitized by ticks (Hart 1992). Such costs involve loss of energy to groom, reduced vigilance against predators, and attrition of teeth (Hart 1990). For moose the cost of intensive grooming to remove embedded nymphal and adult ticks is extensive damage to winter hair in March and April (Mooring and Samuel 1999; Chapters 2 and 3). Such hair loss has not been reported for other tick - host systems. Although free -ranging elk (Mooring and Samuel 1998a) and captive elk and deer (Welch et al. 1991) suffer some hair loss as a result of grooming to remove winter tick larvae, it is not extensive and lost hair is soon replaced. Results of this study and those of Mooring and Samuel (1999) suggest that grooming and resultant hair loss is nutritional and energetically costly for moose.

Negative correlations between rates of grooming and foraging activity for moose in Elk Island National Park suggest the possibility that moose sacrifice feeding time in order to remove ticks during March and April (Mooring and

Samuel 1999; Chapters 2 and 3). Although reduced intake of food at this time could be attributed to normal seasonal declines in forage consumption and metabolism (Schwartz et al. 1987) moose normally consume less food in December and February, not March and April (Renecker and Hudson 1985; Schwartz et al. 1987). Regardless of the difference in timing, which is thought to reflect differences in diets, the winter nadir in food intake is followed by a rapid increase that procedes spring flush by nearly 4 weeks (Renecker and Hudson 1985). Thus, it is unclear to what extent seasonal declines in intake and metabolism influenced the low feeding rate of Elk Island moose.

Because moose are easily heat stressed (Renecker and Hudson 1986a, 1989b, 1990), extensive hair loss in March and April could provide some thermoregulatory benefit from warm spring temperatures (Welch et al. 1990a). Conversely, heat lost from denuded skin may result in reduced visceral fat reserves (Mclaughlin and Addison 1986) and hypothermia (Glines and Samuel 1989). In addition, intensive grooming and hair loss occurs during the last trimester of pregnancy for moose cows. Although no data are available for moose, studies conducted on the energy requirements of gestation in domestic animals show that a growing fetus exerts substantial demands on the mother (Oftedahl 1985 cited in Schwartz and Renecker 1997). For elk the energetic demands of pregnancy suppress body weight gains (Gates and Hudson 1981). Similar demands are likely imposed on pregnant moose. Thus, this cost and the cumulative costs of grooming, hair loss and feeding ticks (blood loss, anemia and the possibility of secondary bacterial infections, Glines and Samuel 1989; Campbell et al. 1994) could put the cow or her unborn calf at risk.

Relationship between winter ticks and moose are complex and several factors other than grooming may influence tick abundance. Adverse weather affects off - host survival of larvae and engorged females. Early snowfall, low temperatures and high winds during autumn decrease survival of tick larvae on vegetation (Samuel and Welch 1991). Wilton and Garner (1993) suggest that a critical mean April temperature between 3 and 4 C might affect tick abundance the following year; i. e., above this temperature survival of engorged females is good and below it survival is poor. This idea is based on results of Drew and Samuel (1986) who showed that survival of engorged female winter ticks was low if they dropped from hosts prior to snowmelt and much higher if they dropped from hosts after snowmelt. They suggested that this might be due to ambient temperature at the snow surface.

Severe weather influences moose mortality as well. Although moose are superbly adapted to cold, and their long legs allow for travel in deep soft snow to locate and reach browse, thick heavy snow crusts and snow depth greater than 60 cm can reduce mobility and access to food (Renecker and Hudson 1992; Renecker and Schwartz 1997).

Weather conditions that adversely affect plant growth can have dire consequences for moose. Basically, moose must feed on high quality forage during summer and autumn in order to accumulate sufficient fat reserves to meet the demands of the breeding season and negative energy balance during winter (Renecker and Hudson 1986b).

Considering the role winter ticks appear to play in morbidity and mortality of moose, a worst case scenario for moose survival would be one in which favorable conditions for winter ticks (i. e., lots of sunny warm days in spring and autumn) result in high numbers of winter ticks while a dry hot summer reduces plant growth and lowers nutritional quality. This is followed by a winter with deep, heavily crusted snow that impedes travel and restricts access to food. Under such conditions moose would enter winter heavily infested with ticks and reduced energy reserves. While heavy infestations of winter ticks on moose entering winter in good body condition may not severely impact most animals, except perhaps young, old, sick, injured or immunocompromised individuals, the same infestation on moose entering winter in poor condition might result in heavy loss of moose as early as January with many more deaths in spring. This scenario appears to be a current reality for overwintering moose in parts of British Columbia and Alberta (W. M. Samuel pers. comm.). If poor quality summer browse and deep snow are the only contributing factors to early winter mortality of moose, one would expect that in winter 1998 - 1999, deer would be dying as well. This does not appear to be happening (W. M. Samuel pers. comm.).

Results of this study add a new dimension to winter tick - moose relationship: the effects of winter ticks on moose behaviour. However, experimental studies are required to further assess the relationship between winter ticks and moose. A good beginning in this area would be a study with an experimental design involving a large group of tame calves paired by sex and weight, one member of which is infested with winter ticks at a density of 1.1 larvae/cm^2 skin surface (i. e., the lowest density reported for wild moose that resulted in hair loss, Samuel and Welch 1991). Food intake and/or food quality would be restricted for some groups. Physiological and nutritional data, weight loss or gains, weather data, grooming rates, hair loss and tick removal data would be collected. Grooming behaviour of wild moose through out the year would be collected to provide baseline data, particularly for grooming that occurs during tick larval attachment. This study could be a springboard to a food - shortage experiment.

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Appendix 1. Moose that escaped during Winter I, 1994 - 1995 and Winter II, 1995 - 1996 from Mud Lake ungulate management facility, Elk Island National Park.

		Treatment group		Total No. observations	
	Moose	Treated	Control	Before	and after escaping
Winter I					
	151.214	x		19	
	151.175	x		28	8
	151.194	x		66	
	150.451	x		66	
	150.288		x	3	
	100.001		x	5	
	151.186		x	19	4
	151.166		x	23	
	151.155		x	54	
Totals				283	12
Winter II					
	w186	x		1	0
	r194	x		37	
	y175	x		55	
	r/s155		x	4	3
Totals				97	3