METABOLIC IMPACTS OF WINTER TICK INFESTATIONS ON CALF MOOSE

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ABSTRACT: Moose (*Alces alces*) are susceptible to late winter mortality from infestation of winter ticks (*Dermacentor albipictus*) throughout much of North America. Calves, perhaps more so than other ages of moose, likely experience chronic, and eventually acute anemia from blood removal by adult female ticks that peaks during weeks 4 – 6 of the 8-week engorgement period. We modeled the potential metabolic impact on protein and energy balance of moose calves associated with blood loss during four levels, low to severe, of winter tick infestation. Our conservative estimates indicated that total blood loss in weeks 4 – 6, as a percent of total blood volume, ranged from 27 to 48% and 64 to 112% during moderate (30,000 ticks) and severe (70,000 ticks) infestations, respectively. The percent of the daily metabolizable energy requirement needed to replace daily blood loss during weeks 4 – 6 was 4.9 – 8.2% and 11.4 – 19.2% during moderate and severe infestations, respectively. The protein deficit associated with blood loss and regeneration was the most critical metabolic impact. Daily protein loss during weeks 4 – 6 was 29 – 49% and 68 – 114% of the daily protein requirement in moderate and severe infestations, respectively. Daily protein losses of ~ 30 to > 100% occurred for 2 continuous weeks. Energy costs associated with compensating for blood loss would likely elevate the daily energy deficit normal at end of winter, accelerate nutritional decline and weight loss, and cause increased physiological stress related to concurrent anemia. Severely infested calves are obviously susceptible to late winter mortality, and the impact of moderate infestations would be exacerbated by secondary parasitic infestations, severe winters, and poor body condition.

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Moose (*Alces alces*), elk (*Cervus elaphus*), and white-tailed deer (*Odocoileus virginianus*) are the three main hosts of the winter tick (*Dermacentor albipictus*) in North America. Moose are the most severely affected from infestations of winter ticks that cause hair loss and damage (McLaughlin and Addison 1986, Samuel 1991), excessive grooming (Mooring and Samuel 1999), chronic weight loss (Glines and Samuel 1989, Addison et al. 1994), and reduced growth and fat stores (McLaughlin and Addison 1986). No reduction in food intake (Addison and McLaughlin 1993) and only one case of tick-induced anemia have been reported for captive moose (Glines and Samuel 1989, Addison et al. 1998b); however, these consequences are more likely to occur in wild moose. Substantial mortality associated with severe tick infestations has occurred throughout much of North American moose range (Samuel 2004). Winter tick related mortality was responsible for 41% (n = 16) of radio-marked mortality in New Hampshire with calves representing 88% of deaths (Musante 2006), although all age classes of moose have been associated with winter tick-related mortality (Samuel and Barker 1979, Pybus 1999, Samuel and Crichton 2003). Presumably, the large volume of blood loss associated with severe tick infestations further reduces nutritional status during March – April when moose normally incur a negative energy deficit (Glines and Samuel 1989, Samuel 2004). Calves are likely the most susceptible cohort and anemia is suspected as the primary factor of mortality.

Disengagement of adult female winter ticks occurs after their final blood meal during a 9 – 10 week period in late February to mid-May, peaking in late March – early April (Drew and Samuel 1989). The duration of feeding for several species of adult female ixodid (hard body) ticks ranges from 6 to 13 days and blood removal can equal 3.0 – 7.5 times their engorged body weight (Sonenshine 1991). Depending on the species and host, engorgement is completed within several days with a large volume of blood loss during the last 24 – 36 hours of feeding. Blood concentration in the cattle tick (*Boophilus microplus*) is greatest during the last hours of final feeding when engorged females consumed a concentrated blood meal twice their own weight (Seifert et al. 1968).

The effect on host fitness associated with blood removal by ectoparasites has been studied in birds (Gold and Dahlsten 1983, Roby et al. 1992, Simon et al. 2003), reptiles (Wikelski 1999), small mammals (Khokhlova et al. 2002), and livestock (Seifert et al. 1968, Springell et al. 1971, Corrier et al. 1979, Norval et al. 1988). These studies indicated that blood consumption by parasites has varying effects on blood protein, weight gain, behavior, productivity, and metabolic rate of hosts. Studies have been conducted involving energetic consequences of tick-induced hair loss and grooming in moose (McLaughlin and Addison 1986, Samuel 1991, Mooring and Samuel 1999); however, little research exists on the relationships among tick infestation, blood loss, and metabolic balance in wild ungulates.

The link between tick infestation and mortality of moose calves is evident; however, the physiological impact on their energy and protein balance has not been estimated quantitatively. Such estimates are useful to understand and predict mortality associated with winter tick infestations. The objective of this study is to estimate the impact of blood loss from winter tick infestations on energy and protein balance of moose calves.

METHODS

Metabolic impacts of blood loss were estimated with models that incorporated variable calf weights, levels of tick infestation, weight of engorged ticks, and timing of feeding. Calf weight in March – April was set at 150 and 175 kg (Samuel 2004), although weights of 11-month-old captive calves may exceed 200 kg (Addison et al. 1994, Broadfoot et al. 1996). Tick infestation level was set as 10,000 (low), 30,000 (moderate), 50,000 (high), and 70,000 (severe) ticks (W.M. Samuel, University of Alberta, personal communication). The number of adult females at each infestation level was estimated as 25.6% of the total tick load as measured on calves in March – April (Samuel 2004). Larvae, nymphs, and adult males were not considered in the analysis, because adult males consume relatively little blood compared to adult females (Sonenshine 1991); and unfortunately, similar data about immature life stages is limited (W.M. Samuel, University of Alberta, personal communication).

Mean engorged weights of adult female ticks have been estimated at 0.61 (Glines 1983) and 0.85 g (Addison et al. 1998a); we used the same conservative estimate of 0.50 g as Samuel (2004) to account for ticks not fully engorged due to early removal by grooming (Drew and Samuel 1989). We assumed that all adult female ticks fed on this amount of blood. Total amount of blood loss per adult female tick does not equal the final engorged weight because undigested blood can be $\geq$2X that of the final engorged weight (Sonenshine 1991); therefore, blood loss was estimated as 2 and 3X engorged weight. Using moose calves experimentally infested with 30,000 larvae, Drew and Samuel (1989) determined that tick drop-off occurred primarily from March to April, peaking between 20 March and 6 April. In the current study the drop-off period and total blood loss was estimated over an 8-week period between 1 March and 25 April; proportional blood loss was estimated as 15% in weeks 0 – 2, 25% in weeks 2 – 4, 50% in weeks 4 – 6, and 10% during weeks 6 – 8.

Vertebrate blood contains approximately 15% hemoglobin and 7% plasma proteins (Sonenshine 1991). Hemoglobin and total protein in blood of moose calves during late winter average 0.17 and 0.06 g/mL, respectively (Franzmann and LeResche 1978). We assumed a conservative value of 0.20 g protein/mL of blood, 4.3 kcal/g protein (Schmidt-Nielson 1997), and a metabolic efficiency of 75% in replacing blood (Blaxter 1989); energetic cost of replacing blood was subsequently estimated as 1.15 kcal/mL. Daily protein requirements were assumed as 168 and 189 g protein/day for 150 and 175 kg calves, respectively (Schwartz et al. 1987, Robbins 1993). Total blood volume was estimated as 8% of body weight (see Samuel 2004); calves weighing 150 and 175 kg had blood volumes of 12,000 and 14,000 mL, respectively. The daily metabolizable energy requirement for maintenance of a calf was assumed as 134 kcal/kg$^{0.75}$/d (Cool and Hudson 1996), which equaled 5,743 and 6,447 kcal/d for a 150 and 175 kg calf, respectively.

RESULTS

Total blood loss at the low infestation level (10,000 ticks) was estimated as 2,560 and 3,840 mL for 2 and 3X engorged weight, respectively; total blood loss at the severe infestation level (70,000) was 17,920 and 26,880 mL, values exceeding total blood volume (Fig. 1). Percent total blood volume lost in 150 and 175 kg calves with low, moderate, high, and severe infestations ranged from 21 to 224% and 18 to 192%, respectively; percent daily blood loss ranged from 0.4 to 4.0% and 0.3 to 3.4%, respectively (Table 1). Percent total blood volume lost in 150 and 175 kg calves with low to severe infestations during weeks

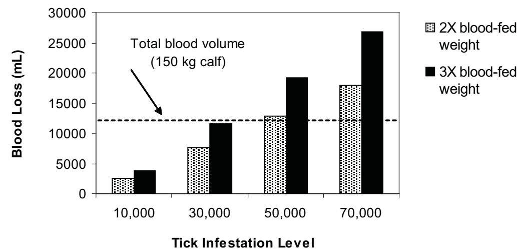

Fig. 1. Total blood removal by adult female winter ticks at low to severe infestation levels on moose calves over the 8-week engorgement period.

4 – 6 ranged from 11 to 112% and 9 to 96%, respectively; percent daily blood loss ranged from 0.8 to 8.0% and 0.7 to 6.9%, respectively (Table 1).

The energy cost to replace blood loss ranged from 2,944 to 20,608 kcal at 2X engorged weight at the four levels of infestation, and 4,416 to 30,912 kcal at 3X engorged weight (Fig. 2). The percent deficit of the daily energy

Table 1. Total and daily percent blood volume of calf moose removed by engorging adult female ticks. Infestation level, stage, engorged weight (2 and 3X), and calf weight were varied; total blood volume was estimated as 8% of body weight.

	Calf Weight (kg)			
	150		175	
Infestation Level	100% Week 0-8	50% Week 4-6	100% Week 0-8	50% Week 4-6
10,000				
2X	21 (0.4)	11 (0.8)	18 (0.3)	9 (0.7)
3X	32 (0.6)	16 (1.1)	27 (0.5)	14 (1.0)
30,000				
2X	64 (1.1)	32 (2.3)	55 (1.0)	27 (2.0)
3X	96 (1.7)	48 (3.4)	82 (1.5)	41 (2.9)
50,000				
2X	107 (1.9)	53 (3.8)	91 (1.6)	46 (3.3)
3X	160 (2.9)	80 (5.7)	137 (2.4)	69 (4.9)
70,000				
2X	149 (2.7)	75 (5.3)	128 (2.3)	64 (4.6)
3X	224 (4.0)	112 (8.0)	192 (3.4)	96 (6.9)

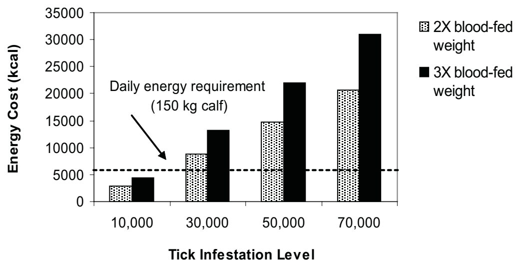

Fig. 2. Total energy cost for moose calves to replace blood loss at low to severe infestation levels of adult female winter ticks over the 8-week engorgement period.

budget for a 150 kg calf ranged from 0.9 to 9.6% for low to severe infestations over 8 weeks, and 1.8 to 19.2% during weeks 4 – 6; the estimates for a 175 kg calf were 0.8 – 8.6% and 1.6 – 17.1%, respectively (Table 2).

Total protein lost during low-to-severe infestations ranged from 512 to 3,584 and 768 to 5,376 g at 2 and 3X blood-fed weight,

Table 2. The cost of replacing blood removed by engorging adult female ticks as a percent of the daily metabolizable energy requirement of moose calves. Infestation level, stage, engorged weight (2 and 3X), and calf weight were varied; total blood volume was estimated as 8% of body weight.

	Calf Weight (kg)			
	150		175	
Infestation Level	100% Week 0-8	50% Week 4-6	100% Week 0-8	50% Week 4-6
10,000				
2X	0.9	1.8	0.8	1.6
3X	1.4	2.7	1.2	2.4
30,000				
2X	2.7	5.5	2.4	4.9
3X	4.1	8.2	3.7	7.3
50,000				
2X	4.6	9.2	4.1	8.2
3X	6.9	13.7	6.1	12.2
70,000				
2X	6.4	12.8	5.7	11.4
3X	9.6	19.2	8.6	17.1

respectively (Fig. 3). Daily protein loss at a moderate infestation level (30,000) and 2-3X blood-fed weight was 11.0 – 16.5 g during weeks 6 – 8 and 54.9 – 82.3 g during weeks 4 – 6 (Fig. 4). Daily protein loss associated with a severe infestation peaked during weeks 4 – 6 and exceeded the daily protein requirement of 150 and 175 kg calves; daily protein loss was 50 – 100% of the daily protein requirement during weeks 2 – 6 (Fig. 4). As a percent of the daily protein requirement during weeks 4 – 6, protein loss of a 150 kg calf peaked at 33 – 49% at a moderate infestation level, and 76 – 114% at a severe infestation level; protein loss of a 175 kg calf peaked at 29 – 44% and 68 – 102% in moderate and severe infestations, respectively (Fig. 4).

DISCUSSION

This exercise, performed with conservative estimates, indicated that blood loss associated with moderate to severe infestations of ticks has substantial impact on energy and protein balance in moose calves. The physiological impact of blood removal by adult female ticks extends for approximately 8 weeks, and calves likely experience chronic, and eventually acute anemia during peak engorgement by weeks 4 – 6 during early to mid-April. Although anemia associated with blood removal by ticks is well recognized in cattle (Francis 1960, O'Kelly and Seifert 1969, Corrier et al. 1979), there is little to no evidence in captive moose (Glines and Samuel 1989, Addison et al. 1998b). Nevertheless, anemia is hypothesized in tick-infested wild moose. Hemorrhagic anemia caused by parasites occurs when the balance between blood loss and production is not maintained, and calves are unable to compensate for blood loss. The protein loss estimates in this study indicate that the potential for hemorrhagic anemia is greatest in weeks 4 – 6 (Fig. 4).

As a consequence of their age and smaller body size, calves have higher metabolic demands than adults on a relative scale

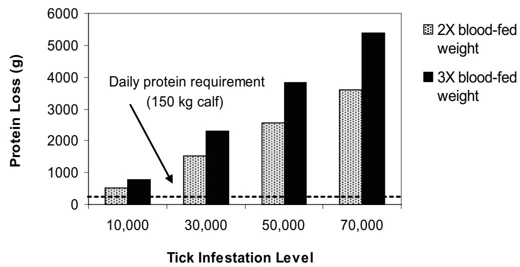

Fig. 3. Total protein cost for moose calves to replace blood loss to adult female winter ticks at low to severe infestation levels over the 8-week engorgement period.

(Schwartz et al. 1991). Stored body fat and protein allow moose to survive normal energetic deficits in late winter (Schwartz and Renecker 1998); however, calves are more susceptible to late winter mortality, because they have proportionally less body fat than adults (Van Ballenberghe and Ballard 1998). During late winter, moose consume forage of minimal nutritional value (Schwartz and Renecker 1998) and the relative energetic cost associated with compensating for blood loss is presumably higher for animals in poor condition, especially calves. Moose calves severely infested or in weakened condition are probably unable to sustain the energetic demand for blood regeneration and consumption of adequate food resources. Volume of daily blood loss was an important factor in the mortality of smaller, tick-infested livestock calves compared to larger surviving calves (Corrier et al. 1979). Tick-infested moose calves that are heavier possibly have a better likelihood of recovery and survival from blood loss. Calves in poor condition may also experience more pronounced energy and protein deficits compared to healthier calves, which likely groom more and should remove a greater number of ticks.

The daily percent loss of total blood volume during weeks 4 – 6 ranged from 2.0 to 3.4% and 4.6 to 8.0%, respectively, during moderate and severe tick infestations of 30,000 and 70,000 ticks (Table 1). Calves infested with $\geq$50,000 ticks would lose 1 – 2X their blood volume over the 8-week engorgement period. Guidelines for blood collection of healthy animals on an adequate nutritional plane suggest that 10% of blood volume can be removed every 3 – 4 weeks or 1% daily for repeated bleeds at shorter intervals (Morton et al. 1993). Further, total blood loss as a percent of total blood volume during weeks 4 – 6 ranged from 27 to 48% and 64 to 112%, respectively (Table 1). Most animals experience hemorrhagic shock if 30 – 40% of blood volume is removed over a short period of time, and > 40% removal may cause death (McGuill and Rowan 1989).

The percent of the daily metabolizable energy requirement required to replace the average daily blood loss during the engorgement period ranged from 2.4 to 4.1% and 5.7 to 9.6% in moderate and severe infestations (Table 2). However, the daily estimates were twice that during weeks 4 – 6 (Table 2), and these additional energy costs would increase the daily energy deficit normal at end of winter, accelerate nutritional decline and weight loss, and likely cause increased physiological stress related to concurrent anemia. Calves normally experience a negative energy balance in winter when the metabolizable energy requirement exceeds forage intake energy; calves sustain a daily energy deficit of about 40% in winter assuming availability of quality dry matter forage (2.2 kcal/g of metabolizable energy) and a daily consumption rate of 1% body weight (Schwartz and Renecker 1998).

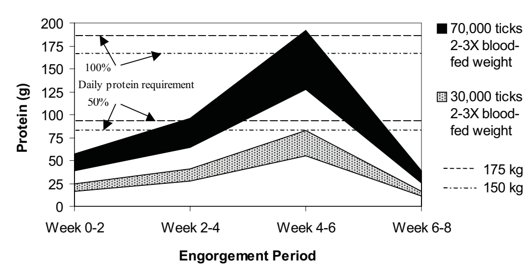

Fig. 4. Daily protein loss in moose calves associated with blood loss at moderate and severe infestation levels of adult female winter ticks over the 8-week engorgement period.

Calves infested with 70,000 ticks would lose an equivalent of 3 – 5 days of metabolizable energy requirement over the 8-week engorgement period. Increased grooming and reduced feeding during March – April accentuate the negative energy balance at the end of winter (McLaughlin and Addison 1986, Samuel 1991, Mooring and Samuel 1999). Although the role of protein metabolism may have the strongest influence on calf survival, the constant energy cost associated with blood replacement adds to the negative impact of ticks.

Low, moderate, and heavy tick numbers had minimal effect on hematological parameters of captive moose maintained on a 16% protein diet (Addison et al. 1998b); however, winter browse typically has 5 – 7% protein and is poorly digested (Schwartz and Renecker 1998). Conversely, poor nutrition reduced hematological values of cattle lightly infested with *Boophilus microplus* compared to those on an adequate diet (O'Kelly et al. 1971), and tick-infested cattle had lower concentrations of hemotacrit, hemoglobin, serum albumin, and total protein than tick-free cattle (O'Kelly and Seifert 1969). Alexander and Kiesel (1965) report that blood loss coupled with low protein diet (8%) adversely affected weight gain, hemoglobin, and hematocrit in lambs; minimal effects occurred in lambs maintained on a 16% protein diet. Thus, the negative impact and host-susceptibility of parasitism in ruminants are greater in malnourished animals; adequate nutrition and protein intake reduce impact (Van Houtert and Sykes 1996, Coop and Kyriazakis 2001).

The protein deficit associated with blood loss and regeneration is probably the most critical physiological problem for calves. In this exercise, daily protein loss of ~ 50 to > 100% of the daily protein requirement of severely infested moose calves occurred for 4 continuous weeks (weeks 2 – 6; Fig. 4). Losses were most pronounced during weeks 4 – 6; 29 – 49% in a moderate infestation and 68 – 114% in a severe infestation (Fig. 4). Calves infested with 70,000 ticks would lose an equivalent of 3 – 4 weeks of the daily protein requirement. Moose are invariably in an energetic deficit and losing weight during winter (Schwartz et al. 1988); therefore, compensation would be problematic, because the engorgement period occurs prior to spring green-up when quality and quantity of forage are limited. Calves experiencing severe blood loss should be considered high-risk mortality from anemia and associated effects. Their ability to survive tick infestations is probably most influenced by their nutritional status and the level of infestation.

The estimated proportion of adult female ticks on adult moose during late winter is lower on cows (18.0%) and slightly higher on bulls (27.6%), relative to calves (25.6%) (Samuel 2004). Based on similar calculations as with calves, the percent daily energy budget deficit associated with a severe infestation level is 4.5 – 6.7% for a cow (360 kg) and 6.3 – 9.5% for a bull (400 kg) during weeks 4 – 6. The percent deficit of the daily protein requirement during a severe infestation is 27.8 – 41.7% for a cow and 39.3 – 59.0% for a bull during weeks 4 – 6. Daily losses in adults, as a proportion of the energy budget and protein requirement, are 50 – 70% less than those estimated for calves. These "baseline" estimates for adults could have greater fitness consequences by compounding the costs of pregnant (last trimester) cows and bulls suffering post-rut. Calves are likely the most susceptible to annual winter tick-related mortality; however, adults in poor condition may be predisposed to mortality from heavy tick infestations or during tick epizootics, although adults should normally survive during years of average tick abundance.

Mortality associated with winter ticks was observed in radio-marked moose in New Hampshire from 2002 to 2005 and was highest in April (75%) corresponding to weeks 4 – 6 of tick engorgement when blood loss was greatest and most concentrated (Musante 2006).

Although tick density was not measured on New Hampshire calves, hair loss and damage was most severe on carcasses in 2002 when calf survival was lowest (0.49) and the highest percentage of tick-related mortality occurred; regional spikes in spring mortality (Samuel and Crichton 2003) and severe coat damage to non-study moose were concurrent. In addition to high and severe levels of infestation and tick-related hair loss/damage, the majority of the calves were emaciated with poor body fat and femur marrow fat ($\bar{x}$ = 16.5%) indices, secondary infestations of lungworm, presumably *Dictyocaulus viviparous*, and noticeable paleness of eye mucous membranes, which is a characteristic of anemia in domestic ruminants (Kaplan et al. 2004).

Dictyocaulus viviparous is found commonly in the small bronchioles of lungs in elk calves, and when combined with severe weather conditions, poor host nutrition, or heavy winter tick infestations, has caused morbidity or death of elk (Worley 1979, Thorne et al. 2002). Although *D. viviparous* is generally not believed related to morbidity of moose (Lankester and Samuel 1998), prevalent infections have been described in calves and yearlings (Pybus 1990). Calf mortalities in Maine during late winter 1995 had infestations of *D. viviparous* and winter ticks (K. Morris, Maine IF&W, personal communication). While this parasite is probably not the primary cause of death, combined infestations of lungworms and winter ticks may be more detrimental than tick infestations alone.

In conclusion, this exercise indicated that blood loss to winter ticks alters protein and energy metabolism of moose calves substantially, and likely influences their fitness and survival. Our models would underestimate the effects associated with more synchronous and concentrated blood loss. Severely infested calves are more susceptible to late winter mortality; however, the effect of a moderate infestation may be amplified by secondary parasitic infestations, severe winters, and poor body condition. The effect of chronic blood loss is exacerbated by a diet of low quality and digestible protein, and as a result, many calves probably are unable to adequately replace blood and protein loss and become acutely anemic. Therefore, it is evident from our conservative estimates and pattern of calf mortality in this study and others, that winter tick infestations and primarily tick epizootics have considerable potential to reduce winter calf survival and influence population dynamics of a local or regional moose population.

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REFERENCES

Addison, E. M., D. G. Joachim, R. F. McLaughlin, and D. J. H. Fraser. 1998a. Ovipositional development and fecundity of *Dermacentor albipictus* (Acari: Ixodidae) from moose. Alces 34:165-172.

_____, and R. F. McLaughlin. 1993. Seasonal variation and effects of winter ticks (*Dermacentor albipictus*) on consumption of food by captive moose (*Alces alces*) calves. Alces 29:219-224.

_____, _____, and J. D. Broadfoot. 1994.

Growth of moose calves (*Alces alces americana*) infested and uninfested with winter ticks (*Dermacentor albipictus*). Canadian Journal of Zoology 72:1469-1476.

_____, _____, and _____. 1998b. Effects of winter tick (*Dermacentor albipictus*) on blood characteristics of captive moose (*Alces alces*). Alces 34:189-199.

ALEXANDER, H. D., and G. K. KIESEL. 1965. The effect of blood loss on weight gain, hemoglobin and hematocrit in lambs fed different levels of protein. Auburn Veterinarian 21:114-117, 129.

BLAXTER, K. L. 1989. Energy Metabolism in Animals and Man. Cambridge University Press, New York, New York, USA.

BROADFOOT, J. D., D. G. JOACHIM, E. M. ADDISON, and K. S. MACDONALD. 1996. Weights and measurements of selected body parts, organs, and long bones of 11-month-old moose. Alces 32:173-184.

COOL, N., and R. J. HUDSON. 1996. Requirements for maintenance and live weight gain of moose and wapiti calves during winter. Rangifer 16:41-45.

COOP, R. L., and I. KYRIAZAKIS. 2001. Influence of host nutrition on the development and consequences of nematode parasitism in ruminants. Trends in Parasitology 29:479-488.

CORRIER, D. E., O. VIZCAINO, M. TERRY, A. BETANCOURT, K. L. KUTTER, C. A. CARSON, G. TREVINO, and M. RISTIC. 1979. Mortality, weight loss and anemia in *Bos taurus* calves exposed to *Boophilus microplus* ticks in the tropics of Columbia. Tropical Animal Health and Production 11:215-221.

DREW, M. L., and W. M. SAMUEL. 1989. Instar development and disengagement rate of engorged female winter ticks, *Dermacentor albipictus* (Acari: Ixodidae), following single- and trickle- exposure of moose (*Alces alces*). Experimental and Applied Acarology 6:189-196.

FRANCIS, J. 1960. The effect of ticks on the growth-rate of cattle. Proceedings of the Australian Society of Animal Production 3:130.

FRANZMANN, A. W., and R. E. LERESCHE. 1978. Alaskan moose blood studies with emphasis on condition evaluation. Journal of Wildlife Management 42:334-351.

GLINES, M. V. 1983. The winter tick, *Dermacentor albipictus* (Packard, 1896): Its life history, development at constant temperatures, and physiological effects on moose, *Alces alces* L. M.Sc. Thesis, University of Alberta, Edmonton, Alberta, Canada.

_____, and W. M. SAMUEL. 1989. Effect of *Dermacentor albipictus* (Acari: Ixodidae) on blood composition, weight gain and hair coat of moose, *Alces alces*. Experimental and Applied Acarology 6:197-213.

GOLD, C. S., and D. L. DAHLSTEN. 1983. Effects of parasitic flies (*Protocalliphora* spp.) on nestlings of mountain and chestnut-backed chickadees. Wilson Bulletin 95:560-572.

KAPLAN, R. M., J. M. BURKE, T. H. TERRILL, J. E. MILLER, W. R. GETZ, S. MOBINI, E. VALENCIA, M. J. WILLIAMS, L. H. WILLIAMSON, M. LARSEN, and A. F. VATTA. 2004. Validation of the FAMACHA© eye color chart for detecting clinical anemia in sheep and goats on farms in the southern United States. Veterinary Parasitology 123:105-120.

KHOKHLOVA, I. S., B. R. KRASNOV, M. KAM, N. I. BURDELOVA, and A. A. DEGEN. 2002. Energy cost of ectoparasitism: the flea *Xenopsylla ramesis* on the desert gerbil *Gerbillus dasyurus*. Journal of Zoology, London 258:349-354.

LANKESTER, M. W., and W. M. SAMUEL. 1998. Pests, parasites and diseases. Pages 479-517 *in* A. W. Franzmann and C. C. Schwartz, editors. Ecology and Management of the North American Moose. Smithsonian Institution Press, Washington, D.C., USA.

McGuill, M. W., and A. N. Rowan. 1989. Biological effects of blood loss: implications for sampling volumes and techniques. Institute for Laboratory Animal Research News 31:5-18.

McLaughlin, R. F., and E. M. Addison. 1986. Tick (*Dermacentor albipictus*)-induced winter hair-loss in captive moose (*Alces alces*). Journal of Wildlife Diseases 22:502-510.

Mooring, M. S., and W. M. Samuel. 1999. Premature winter hair loss in free-ranging moose (*Alces alces*) infested with winter ticks (*Dermacentor albipictus*) is correlated with grooming rate. Canadian Journal of Zoology 77:148-156.

Morton, D. B., D. Abbot, R. Barclay, B. S. Close, R. Ewbank, D. Gask, M. Heath, S. Mattic, T. Poole, J. Seamer, J. Southee, A. Thompsan, B. Trussel, C. West, and M. Jennings. 1993. Removal of blood from laboratory animals and birds. Laboratory Animals 27:1-22.

Musante, A. R. 2006. Characteristics and dynamics of a moose population in northern New Hampshire. M.Sc. Thesis, University of New Hampshire, Durham, New Hampshire, USA.

Norval, R. A. I., R. W. Sutherst, J. Kurki, J. D. Gibson, and J. D. Kerr. 1988. The effect of the brown ear-tick *Rhipicephalus appendiculatus* on the growth of Sanga and European breed cattle. Veterinary Parasitology 30:149-164.

O'kelly, J. C., R. M. Seebeck, and P. H. Springell. 1971. Alterations in host metabolism by the specific and anorectic effects of the cattle-tick (*Boophilus microoplus*). II. Changes in blood composition. Australian Journal of Biological Sciences 24:381-389.

_____, and G. W. Seifert. 1969. Relationships between resistance to *Boophilus microplus*, nutritional status, and blood composition in Shorthorn x Hereford cattle. Australian Journal of Biological Sciences 22:1497-1506.

Pybus, M. J. 1990. Survey of hepatic and pulmonary parasites of wild cervids in Alberta, Canada. Journal of Wildlife Diseases 26:453-459.

_____. 1999. Moose and ticks in Alberta: a dieoff in 1998/99. Occasional Paper Number 20, Fisheries and Wildlife Management Division, Edmonton, Alberta, Canada.

Robbins, C. T. 1993. Wildlife Feeding and Nutrition, Second edition. Academic Press, New York, New York, USA.

Roby, D. D., K. L. Brink, and K. Wittmann. 1992. Effects of blowfly parasitism on eastern bluebird and tree swallow nestlings. Wilson Bulletin 104:630-643.

Samuel, B. 2004. White as a Ghost: Winter Ticks & Moose. Natural History Series, Volume 1. Federation of Alberta Naturalists, Edmonton, Alberta, Canada.

Samuel, W. M. 1991. Grooming by moose (*Alces alces*) infested with the winter tick, *Dermacentor albipictus* (Acari): A mechanism for premature loss of winter hair. Canadian Journal of Zoology 69:1255-1260.

_____, and M. Barker. 1979. The winter tick, *Dermacentor albipictus* (Packard, 1869) on moose *Alces alces* (L.), of central Alberta. Proceedings of the North American Moose Conference and Workshop 15:303-348.

_____, and V. Crichton. 2003. Winter ticks and winter-spring losses of moose in western Canada, 2002. The Moose Call 16:15-16.

_____, and D. A. Welch. 1991. Winter ticks on moose and other ungulates: factors influencing their population size. Alces 27:169-182.

Schmidt-Neilsen, K. 1997. Animal Physiology: Adaptation and Environment. Fifth edition. Cambridge University Press, New York, New York, USA.

Schwartz, C. C., M. E. Hubbert, and A. W. Franzmann. 1988. Energy requirements of adult moose for winter maintenance. Journal of Wildlife Management 52:26-33.

_____, _____, and _____. 1991. Energy expenditure in moose calves. Journal of Wildlife Management 55:391-393.

_____, W. L. Regelin, and A. W. Franzmann. 1987. Protein digestion in moose. Journal of Wildlife Management 51:352-357.

_____, and L. A. Renecker. 1998. Nutrition and energetics. Pages 441-478 *in* A. W. Franzmann and C. C. Schwartz, editors. Ecology and Management of the North American Moose. Smithsonian Institution Press, Washington, D.C., USA.

Seifert, G. W., P. H. Springell, and R. J. Tatchell. 1968. Radioactive studies on the feeding of larvae, nymphs, and adults of the cattle tick, *Boophilus microplus* (Canestrini). Parasitology 58:415-430.

Simon, A., D. W. Thomas, J. R. Speakman, J. Blondel, P. Perret, and M. M. Lambrechts. 2003. Impact of ectoparasitic blowfly larvae (*Protocalliphora* spp.) on the behavior and energetics of nestling blue tits. Journal of Field Ornithology 76:402-410.

Sonenshine, D. E. 1991. Biology of Ticks. Volume I. Oxford University Press, New York, New York, USA.

Springell P. H., J. C. O'Kelly, and R. M. Seebeck. 1971. Alterations in host metabolism by the specific and anorectic effects of the cattle tick (*Boophilus microplus*). III. Metabolic implication of blood volume, body water, and carcass composition changes. Australian Journal of Biological Sciences 24:1033-1045.

Thorne, E. T., E. S. Williams, W. M. Samuel, and T. P. Kistner. 2002. Diseases and parasites. Pages 351-387 *in* D. E. Toweill and J. W. Thomas, editors. North American Elk: Ecology and Management. Smithsonian Institution Press, Washington, D.C., USA.

Van Ballenberghe, V., and W. B. Ballard. 1998. Population dynamics. Pages 223-245 *in* A. W. Franzmann and C. C. Schwartz, editors. Ecology and Management of the North American Moose. Smithsonian Institution Press, Washington, D.C., USA.

Van Houtert, M. F. J., and A. R. Sykes. 1996. Implications of nutrition for the ability to withstand gastrointestinal nematode infections. International Journal of Parasitology 26:1151-1168.

Wikelski, M. 1999. Influences of parasites and thermoregulation on grouping tendencies in marine iguanas. Behavioral Ecology 10:22-29.

Worley, D. E. 1979. Parasites and parasitic diseases of elk in northern Rocky Mountain region: A review. Pages 206-211 *in* M. S. Boyce and L. D. Hayden-Wing, editors. North American Elk: Ecology, Behavior, and Management. University of Wyoming, Laramie, Wyoming, USA.