

ADAPTATIONS OF WINTER TICKS (*DERMACENTOR ALBIPICTUS*) TO INVADE MOOSE AND MOOSE TO EVADE TICKS

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ABSTRACT: Most North American moose (*Alces alces*) outside Newfoundland and south of 60° N latitude are infested annually with winter ticks, *Dermacentor albipictus*. Moose commonly are host to many thousand winter ticks, and tick-associated die-offs of moose are reported often. Larval winter ticks display such behavior as aggregating in clumps on the leeward side of vegetation at heights of preferred ungulate hosts, apparently aiding in their survival and in contacting vertebrate hosts. Moose, in turn, avoid or reduce infestation by ticks by evading tick larvae on vegetation, tolerating tick-foraging by magpies, and grooming to remove ticks. Recent evidence that grooming by African antelope and North American bison and wapiti is regulated by a centrally controlled mechanism that acts to evoke preventive grooming before ticks can attach and feed, has not been supported for moose. This paper reviews host-finding adaptations of winter ticks, pathogenic characteristics of winter ticks for moose, the relationship between magpies and moose, and the biological basis of grooming in moose.

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In a typical interaction between a parasite and its vertebrate host, the parasite uses a variety of morphological, physiological, and behavioral adaptations to acquire a host and to survive and reproduce successfully on that host. The host, in turn, has evolved defenses, including immunological and behavioral responses that will regulate numbers of parasites (Kim 1985, Hart 1990). Usually this co-evolutionary 'arms race' works well, and there is equilibrium between parasite and host wherein numbers of parasites are relatively few on or in most hosts, and death of hosts is rare. In other cases it appears that the host has not yet evolved the necessary defense mechanisms to co-exist with the parasite without death

of the host. Moose (*Alces alces*) with winter ticks (*Dermacentor albipictus*) appear to fit this latter category.

This paper examines host-seeking adaptations of winter ticks, invasive characteristics displayed by winter ticks, and behavioral defenses of moose to winter ticks.

THE TICK

Packard (1869) originally described winter tick, *Dermacentor albipictus*, from a moose from Nova Scotia. Since then, *D. albipictus* has been reported from many species of mammals in North America (Gregson 1956), but members of the *Cervidae*, particularly moose, wapiti

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(*Cervus elaphus*), and deer (*Odocoileus* spp.), are the major hosts. Winter ticks occur on moose throughout much of moose range in Canada south of approximately 60° N latitude (Gregson 1956), and in the contiguous United States (Anderson and Lankester 1974, Samuel and Welch 1991). They are present but not common on moose of the southern Yukon Territory (Samuel 1989), but are not known from Alaska (Zarnke *et al.* 1990) or Newfoundland.

Dermacentor albipictus is a 1-host tick; i.e., all parasitic life stages, larva, nymph, and adult, occur on the same host individual. Growth and development of winter ticks on Canadian moose follow a predictable annual pattern based on results of studies of captive infested moose (Addison and McLaughlin 1988, Drew and Samuel 1989, Welch *et al.* 1991) and field studies (Drew and Samuel 1985, 1986, Samuel 1988). Larvae climb vegetation and form in aggregations in late summer-early autumn. Moose become infested from September to early November when they touch vegetation with larvae. Larvae feed and molt to nymphs within 3 weeks of infestation. Nymphs enter a diapause during October-November that varies in length, but usually ends in late January. Nymphs feed and molt to adults between January and March, and adult females engorge on blood during March and April, then drop from moose. They lay eggs in leaf litter in late May-early June and eggs hatch to larvae in summer. Thus, there is 1 generation of ticks per year, and in the North the timing of the life cycle appears to vary little between years or locations (Lankester and Samuel 1998). In southern areas such as Texas and California, the parasitic phase of the life cycle can be approximately 5 months shorter than that in Alberta (Addison and McLaughlin 1988).

Winter ticks are prevalent in many populations of North American deer, elk,

and moose (Pederson 1977, Durden *et al.* 1991, Samuel *et al.* 1991, Amerasinghe *et al.* 1992, Gill *et al.* 1993). They tend to be more numerous on moose, less so on elk and deer. It appears that where winter ticks occur in western North America, most animals are infested annually. For example, in Elk Island National Park (EINP), Alberta, all of 95 moose and 36 elk, 8 of 10 white-tailed deer (*Odocoileus virginianus*), and 7 of 8 bison (*Bison bison*), collected 1980 - 1990, were infested (WMS, Univ. Alberta, *unpubl. data*). All of 22, 57, and 29 moose from northern British Columbia, Manitoba, and central Alberta (excluding EINP), respectively, were infested (Samuel and Welch 1991). Winter tick-induced hair damage from grooming was observed on 89% of 724 moose from 9 sites in Maine, Utah, Wyoming, Manitoba, and Alberta (Samuel and Welch 1991).

HOST-SEEKING ADAPTATIONS

Ticks use 1 of 2 main strategies to find hosts; they either hunt them or ambush them (Waladde and Rice 1982). Winter tick larvae 'ambush' hosts in autumn by positioning themselves on vegetation and 'waiting' for hosts to pass nearby. Although relatively little is known about movement of winter ticks to a host-contact position on vegetation, winter ticks display several behaviors that likely increase their chances of contacting moose and other cervids.

Winter tick larvae cease climbing and form aggregations at or near tips of vegetation (Fig. 1) at heights of preferred cervid hosts (Fig. 2), rather than positioning themselves on vegetation at random (McPherson *et al.* 2000). When McPherson *et al.* (2000) released larvae at the base of simulated vegetation (245 cm-tall nylon rods), 82% of 434 clumps were between 50 cm (chest height of deer) and 190 cm (shoulder height of moose), thus facilitating contact with the torso of deer, elk, and moose. Only

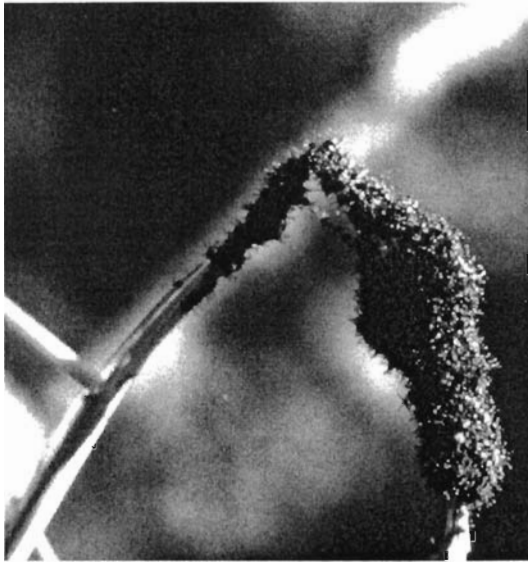


Fig. 1. A large aggregation of questing larvae of winter ticks (*Dermacentor albipictus*), in typical ‘ambush’ position at tip of vegetation in autumn.

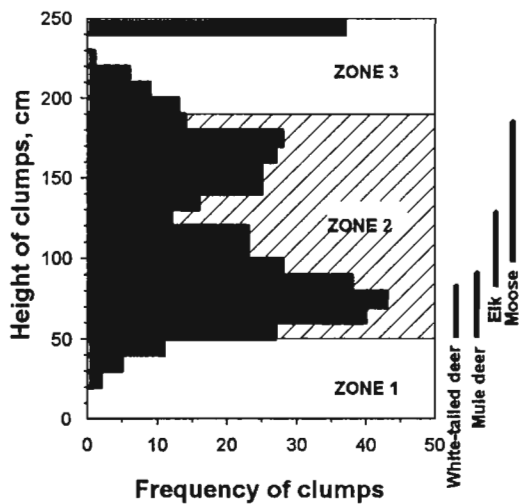


Fig. 2. Frequency distribution of clumps of larvae of *Dermacentor albipictus* with respect to heights of ungulate hosts. Data from McPherson *et al.* (2000). Dashed lines represent mean chest heights for juvenile (50.1 cm) and adult mule and white-tailed deer (61 cm), elk (85 cm), and moose (105 cm). Solid lines represent mean shoulder heights for mule and white-tailed deer (91 cm), elk (129 cm), and moose (190 cm).

18 clumps formed below 50 cm, which is in agreement with Drew and Samuel (1985) and Aalangdong (1994) who found no clumps of larvae on vegetation in EINP, below 20 and 45 cm, respectively. It is not known whether or not winter tick larvae actively select certain species of plants, or individual branches, but Lane *et al.* (1985) found that *Dermacentor occidentalis* did not prefer one species of chaparral shrub over another.

Larvae tend to clump on the leeward sides of vegetation (Aalangdong 1994, Fig. 3), possibly to avoid desiccation and being dislodged by wind. During autumn in central Alberta, the strongest winds generally blow from the northwest and average over 20 km/hr, while the most persistent (but milder) winds blow from the south (Olson 1985). Aalangdong (1994) inferred that solar radiation was not as important as wind in influencing the location of clumps on vegetation, because position of clumps on stems of vegetation did not change by day, cloudy or bright, or with change in the position of the sun.

Larvae remain intact and at the same host-contact position on vegetation continu-

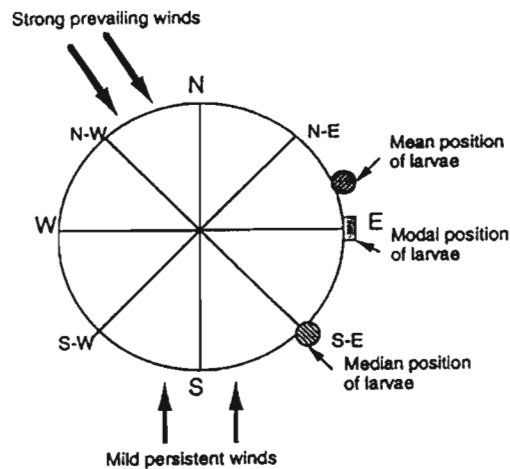


Fig. 3. Position of larvae of winter ticks on vegetation in relation to wind direction in young aspen habitat in Elk Island National Park, Alberta (data from Aalangdong 1994).

ously except when they transfer to a host, are blown off, get covered with snow, or die (Samuel and Welch 1991). They are not like some species of ticks, which make diurnal, vertical migrations from vegetation to the soil-litter interface to replenish water (Lees and Milne 1951, Knulle and Rudolph 1982). Cutcher (1973) and Loye and Lane (1988) suggest that clumping by ticks improves survival by increasing "microclimatic humidity."

Larvae are most numerous on vegetation (Drew and Samuel 1985) and become active quickly in response to stimulation (Aalangdong 1994, Figs. 4 and 5) from late September through early November, which coincides with the mating seasons of moose (Lent 1974), and wapiti (*Cervus elaphus canadensis*), and deer (*Odocoileus* spp.) in Alberta (Stelfox and Stelfox 1993). During this time, rutting males court females and, in the process, both sexes, but particu-

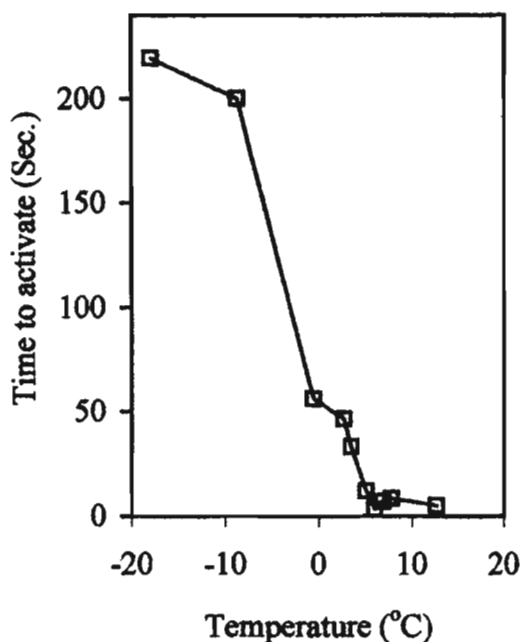


Fig. 4. Mean time (sec) from inactivity to questing by larvae of *Dermacentor albipictus*, following exposure to human breath, at various ambient temperatures in a stand of young aspen habitat, Elk Island National Park, Alberta (data from Aalangdong 1994).

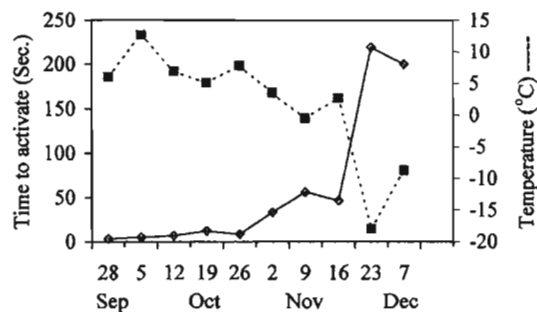


Fig. 5. Mean time (sec) from inactivity to questing by larvae of *Dermacentor albipictus* following exposure to human breath, 28 September to 7 December 1992, in a stand of young aspen, Elk Island National Park, Alberta (data from Aalangdong 1994).

larly males, cover large areas of potentially tick-infested habitat.

Meteorological factors (e.g., temperature, wind, snow) affect numbers (Drew and Samuel 1985, Samuel and Welch 1991) and activity of larvae (Aalangdong 1994). Clumped larvae are normally stationary and inactive with forelegs folded and other legs holding to other larvae or vegetation. When stimulated with human breath, those at the surface become active and wave their front legs (seen as irregular surface outline of clump shown in Fig. 1). Aalangdong (1994) found that time from inactivity to activity was negatively correlated with ambient temperature ($r = -0.84$, $P < 0.001$), being longer at low temperatures than at high temperatures (Fig. 4) and positively correlated with date (= age of larvae) ($r = 0.77$, $P < 0.001$) (Fig. 5) and wind ($r = 0.22$, $P = 0.015$). Generally, at or $< 0^{\circ}\text{C}$, more than 1 bout of human breath was required to activate larvae. At lower temperatures ($< -10^{\circ}\text{C}$), more than 2 bouts of human breath stimulation were required to activate tick larvae and response times were several minutes. The positive correlation between response time and progression of the transmission season (i.e., date), even when the effect of temperature was removed, was attributed to aging of the larvae (Aalangdong 1994).

As tick larvae age, energy reserves are depleted (Lees and Milne 1951; Gray 1985, 1991; Steele and Randolph 1985). Larvae likely go from inactivity to activity many times during their life; as energy stores are depleted, so too is the ability of larvae to respond to host stimuli.

Hind legs of larvae in clumps appear interlocked (WMS, Univ. Alberta, *pers. observ.*), thus potentially facilitating transfer of many larvae to a vertebrate host that contacts a few larvae at the surface of a clump.

In summary, ambushing adaptations of winter tick larvae, and synchrony of larvae and moose activities, play a major role in transmission of winter ticks from vegetation to moose. These adaptations appear to be particularly important in northern regions where the period of transmission is often shortened by the early arrival of winter.

INVASIVE CHARACTERISTICS OF WINTER TICKS FOR MOOSE

One feature of the winter tick - moose relationship, at least in western Canada, is the overwhelming numbers of winter ticks found on moose. Total mean numbers of ticks estimated from digestion of half-hides using techniques described by Welch and Samuel (1989) were 30,683 ($\pm 24,131$ SD) (range 2,774 - 149,916) for 183 moose shot between October and April during the years 1980 - 1990 (WMS, Univ. Alberta, *unpubl. data*). Moose were from northern British Columbia ($n = 22$), Elk Island National Park (EINP) (82) and near Rochester (20), central Alberta, 2 sites in central Alberta (3), and Manitoba (56). The median number of ticks for these moose was 25,518 (WMS, Univ. Alberta, *unpubl. data*). Tick numbers from 22 moose found dead from November to April during the years 1981 - 1989 were 44,748 ($\pm 37,933$ SD) (range 6,626 - 144,542) (median = 25,964) (WMS, Univ. Alberta, *unpubl. data*). Moose were

from EINP ($n = 13$), 4 sites in central Alberta (6), Manitoba (1), and Isle Royale National Park, Michigan (2).

Total mean numbers of ticks (estimated as described above) from sympatric hosts in EINP were 1,200 (15 wapiti), 540 (6 white-tailed deer) (Welch *et al.* 1991), and 133 (9 bison) (Mooring and Samuel 1998b). In other words, based on estimated mean numbers, moose had at least 230 times more ticks per animal than bison, yet mass of bison is ~ 1.5 times that of moose. Mooring and Samuel (1998a) estimated that an average 6,842 ticks (5,922 nymphs and 920 adults) engorged on moose each day during March - April, based on mean intensity of 28,065.

Several experimental studies (see papers cited below) support the supposition that winter ticks have a detrimental effect on moose fitness. Tick-caused problems documented for moose include:

1. destruction of the winter hair coat (McLaughlin and Addison 1986, Samuel *et al.* 1986) (Fig. 6), the result of grooming (Samuel 1991; Mooring and Samuel 1998a, 1999);
2. negative association of time spent grooming with time spent feeding (suggests that moose sacrifice feeding to remove ticks) (Mooring and Samuel 1999, DelGiudice *et al.* 1997);
3. restlessness (Samuel 1991);
4. anemia and other physiological effects (Glines and Samuel 1989);
5. reduced visceral fat stores (McLaughlin and Addison 1986);
6. reduced growth in young moose (Addison *et al.* 1994); and
7. tick-related morbidity and mortality (Timmermann and Whitlaw 1992, Lankester and Samuel 1998).

Moose in experimental studies have been infested with numbers of ticks seen typically on wild moose, and compared with uninfested moose that differed from in-

fested moose only in not having ticks. In total this information suggests that infestations of *D. albipictus* often harm moose. In fact, at this point in the 'arms race' between host and parasite there is little evidence that winter ticks pay much of a price for killing moose, although one obvious result of a large die-off of moose is a smaller host population for the tick in future years.

On the other hand, several experimental studies suggest that winter ticks have little effect on some aspects of moose physiology or behavior. Welch *et al.* (1990) found that tick-induced alopecia (Fig. 6) had no demonstrable effect on the fasted metabolic rates of captive moose when ambient winter - spring temperatures were

mild (-3 to +33°C). They noted that tick-induced alopecia may impose only nominal thermoregulatory costs on wild moose simply because hair loss on infested moose is rarely extensive before March and moose do not usually experience prolonged periods of severe cold after March. In addition, anorexia, which is induced by some species of ticks in some hosts (e.g., Seebeck *et al.* 1971), did not occur in captive moose calves (Glines and Samuel 1989, Addison and McLaughlin 1993). Addison *et al.* (1998) found "limited impact of ticks on hematological and biochemical parameters of well-fed captive moose." In summary, this issue is complicated no matter if one is attempting to evaluate studies of moose infested experimentally with ticks (Welch 1988, Welch *et al.* 1990, Addison and McLaughlin 1993) or evaluating the role of winter ticks in survival of wild moose. For more on this see DelGiudice *et al.* (1997).

HOW MOOSE EVADE WINTER TICKS

The role of animal behavior in the control of parasites has been studied extensively (Hart 1990, 1992, 1994). In this paper we review briefly several behavioral adaptations used by moose to reduce numbers of winter ticks. We contend that, although these adaptations affect tick numbers on moose, they are not yet well developed for moose, at least when compared with other winter tick - host systems. Behavioral patterns that moose use to defend against *D. albipictus* can be termed the "parasite avoidance strategy" (Hart 1990). They enable moose to avoid or minimize exposure to ticks and include moose movement to avoid larval ticks on vegetation, toleration of foraging by birds of the family Corvidae to minimize exposure to ticks, and self-grooming to remove ticks.

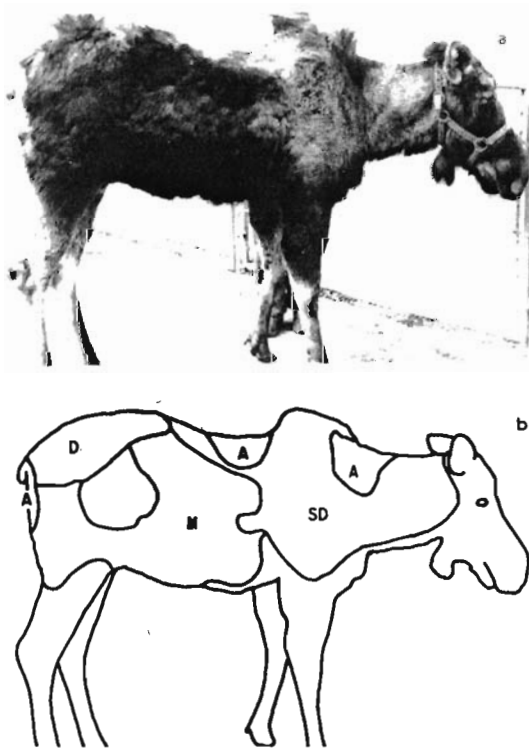


Fig. 6. Pattern of tick-induced hair destruction on the torso of a moose infested with 50,000 larvae of *Derma-centor albipictus* (a), and a schematic classification of damaged hair (b). D = Disturbed, M = Mottled, SD = Severely Damaged, A = Hair Absent. (from Welch 1988).

Avoiding Ticks

As moose and other wild ungulates move and forage through vegetation, they are annually exposed to thousands of winter tick larvae. Do they detect and avoid larvae, thereby reducing exposure to tick larvae? In a pilot experiment, Samuel and Welch (1991) found that a captive moose avoided pelleted food on which many winter-tick larvae had been placed. Hewetson (1968) and Sutherst *et al.* (1986) reported that cattle either refused to graze in small experimental paddocks seeded with larvae of the tick *Boophilus microplus* or they avoided small areas of pasture seeded with many tick larvae. Photographs in Sutherst *et al.* (1986) show that cattle "changed direction abruptly on entering tick-infested circular plots," or made "no response" in tick-free plots. Cattle exhibited a state of increased alertness following apparent visual detection of the dark brown larvae on grass (Sutherst *et al.* 1986). The captive moose became very agitated following apparent visual detection of tick larvae on pelleted food (WMS, Univ. Alberta, *pers. observ.*).

Toleration of Tick-Feeding by Magpies

The symbiotic relationship between oxpeckers (*Buphagus* spp.), the world's only obligate tick bird, and their African ungulate hosts, is well known. By eating ticks, oxpeckers gain a major food item, and hosts have reduced numbers of ticks. The average bird can have 400 ticks in its stomach, and efficiency at removing ticks from individual hosts often exceeds 90 % (Bezuidenhout and Stutterheim 1980). One would predict that some species of African vertebrates, with large numbers of ticks, have evolved behavior facilitating foraging by oxpeckers. Indeed, oxpeckers are known to forage on the largest available hosts that support higher densities of ticks than smaller hosts (Mooring and Mundy 1996a). They also feed primarily on parts of the body

(e.g., ears, neck, perianal region) that impala cannot reach by oral grooming and where tick densities are highest (Mooring and Mundy 1996b).

When presented the opportunity, members of the family Corvidae prey on winter ticks on a variety of ungulates, including moose (Addison *et al.* 1989, Samuel and Welch 1991). Birds involved include gray jays (*Perisoreus canadensis*) and common ravens (*Corvus corax*) (Addison *et al.* 1989), black-billed magpies (*Pica pica*) (WMS, Univ. Alberta, *pers. observ.*), and perhaps, scrub jays (*Aphelocoma coerulescens*) (Isenhardt and DeSante 1985). Corvids either attend and feed on ticks on hosts such as mule deer (*Odocoileus h. hemionus*) (Fig. 7), or forage on the ground at a moose bedding site (Addison *et al.* 1989; WMS, Univ. Alberta, *pers. observ.*). Although the winter tick-cervid-corvid system is much different than the tick-African vertebrate-oxpecker example (e.g., corvids are not obligate tick-feeders, but rather opportunistic feeders and scatter hoarders that cache food at scattered locations; Trost 1999), vertebrate hosts such as wapiti, moose, and mule deer tolerate magpies apparently tick-feeding in or on their ears and on their side and back (WMS, Univ. Alberta, *pers. observ.*; Fig. 7).

Studies are needed to determine whether magpies feed preferentially on moose, the host with high densities of winter ticks, rather than hosts with fewer ticks (e.g., wapiti), particularly when adult ticks are numerous in March and April. Magpies might choose to minimize search time for ticks by feeding on wapiti that often occur in groups, rather than moose that tend to be solitary. Because of the presence of their "hump", moose cannot oral groom certain areas of the body as can deer and elk. One might suggest that magpies or other corvids take advantage of this by feeding preferen-



Fig. 7. Magpies apparently feeding on winter ticks on mule deer fawns, southern Alberta (picture courtesy Frank de Boon).

tially on areas of the body where moose cannot groom and thus, where tick densities are highest.

Self Grooming to Remove Ticks

Anderson and Lankester (1974) and Welch *et al.* (1991) suggested that moose were poorly adapted to winter ticks. Specifically “moose may be much less successful than deer in removing the parasites [winter ticks] by rubbing and grooming behavior” (Anderson and Lankester 1974) and “grooming by deer and by elk [wapiti] may have been more effective [than moose] in removing ticks” (Welch *et al.* 1991).

Mooring and Samuel (1998a, b, c, 1999) applied ideas on tick-removal grooming by African antelope (Hart *et al.* 1992, Mooring 1995, Mooring *et al.* 1996) to moose, bison, and wapiti. They assumed that the costs of hosting ticks, well documented for cattle (Little 1963, Sutherst *et al.* 1983, Norval *et al.* 1988, Kaiser *et al.* 1991), apply to wild hosts such as moose. Mooring and Samuel (1998a, 1999) provide evidence that moose groom primarily in response to the cutaneous irritation associated with tick bite (i.e., the ‘stimulus-driven’ model). That is, moose groom most intensively in March and April when adult ticks are feeding. This is in contrast to tick-grooming in African antelope, bison, and wapiti, in which the groom-

ing response appears to be centrally controlled (neurobiological control), with the host ‘anticipating’ the occurrence of ectoparasites such as ticks, and removing them in a preventative manner before they attach and feed. The mechanism has been termed ‘programmed grooming’ (Hart *et al.* 1992). Preventive grooming would appear to be more adaptive than stimulus-driven grooming.

Why would moose be the exception to the programmed-grooming model? Mooring and Samuel (1998a) suggest that moose groom ineffectively against winter ticks because the evolutionary relationship between moose and winter ticks is relatively recent. That is, there has been insufficient time for moose to mount an evolutionary response to winter tick infestation. Anderson and Lankester (1974) suggest that moose, a relatively recent arrival to North America (Bubenik 1998), acquired some of their parasites, most notably meningeal worm (*Parelaphostrongylus tenuis*), liver fluke (*Fascioloides magna*), and winter tick, from “strictly native cervids of the genus *Odocoileus*.” None of these parasites is known from the Old World, and each appears to be a parasite that has spread from a host in which it has a long association (i.e., host is well adapted and parasite is relatively benign) to a ‘new’ host in which it has a relatively short association (i.e., host is poorly adapted and parasite is relatively pathogenic) (Anderson and Lankester 1974, Holmes 1996).

In summary, grooming is probably the most important behavioral strategy used by moose against infestations of winter ticks, but moose are not nearly as efficient as deer and elk at reducing numbers of ticks by grooming (Welch *et al.* 1991). It appears that winter ticks might have spread from deer, the more widespread and numerous host, to moose, in which there is much less selection for reduced pathogenicity (Price

et al. 1986, Holmes 1996).

CONCLUSIONS

Although infestation with ticks in wild-life is generally not dramatic, moose with infestations of winter ticks appear to be an exception. Winter ticks are well adapted to ambush moose, and moose have not yet evolved efficient defenses against them. The result is high numbers of ticks on moose and frequent mortality of moose. Little is known about moose avoiding ticks in the environment or tolerance of moose to tick-foraging by magpies and other members of the Corvidae as a strategy for tick removal. If, for example, magpies remove significant numbers of ticks, particularly from body regions relatively inaccessible to grooming, natural selection should favor evolution of host behavior patterns that facilitate foraging efficiency by magpies. Grooming is probably the most important behavioral strategy used by moose against winter ticks, but other hosts appear to be more effective than moose at removing ticks by grooming.

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