MATURE CONIFEROUS FOREST AS CRITICAL MOOSE HABITAT

Stephen Balsom[1], Warren B. Ballard[1,2], and Heather A. Whitlaw[1]

[1]New Brunswick Cooperative Fish and Wildlife Research Unit, University of New Brunswick, P. O. Box 44555, Fredericton, NB E3B 6C2; [2]Present address and address to which reprint requests should be sent: Arizona Game and Fish Department, 2221 West Greenway Road, Phoenix, Arizona 85023

ABSTRACT: We reviewed literature on the use of mature coniferous forest habitat by moose (*Alces alces*) for evidence that this habitat was critical to moose survival and reproduction. To be considered critical for moose, it would have to be demonstrated that either reduction or elimination of this forest type resulted in lower reproduction, higher mortality, or both in relation to a control area (White and Garrot 1991). We found no studies of this type which would be necessary to prove that mature coniferous habitat was critical to moose.

ALCES VOL. 32 (1996) pp.131-140

Today's increased demands on natural resources are impacting upon wildlife habitat through removal and changes in landscape dynamics (Ontario Ministry of Natural Resources [OMNR] 1988). As this demand increases, the need for accurate and reliable information on habitat as a limiting factor to animal populations also increases. Now more than ever, managers need to know the importance of specific habitat types to wildlife populations, in addition to understanding how changes to, or the removal of, these habitat types will affect a wildlife population.

Mature coniferous forest habitat types and their importance to moose populations have been studied for many years. The accepted idea that mature coniferous habitat is necessary for the survival and reproduction of moose has become a consideration in the forest industry and in forest management practices (OMNR 1988). Studies of mature coniferous habitat have examined its role in providing cover, forage, and protection from predation during various seasons (Kelsall and Telfer 1974, Peterson 1977, Ballard *et al.* 1991). Conclusions have been based primarily on observations and preference studies which compare availability and usage data. However, these types of studies tell us nothing about habitats utilized by the animal as being critical to survival and reproduction. The only approach to determine criticalness of a habitat type is through manipulative study.

One method to determine criticalness of a habitat would be to restrict or prohibit the population's access to the habitat, monitor survival and reproduction, and compare the results to a control area (White and Garrot 1991). A decline in reproduction or moose population density, or increased mortality, as a result of these restrictions would provide evidence of the criticalness of the mature coniferous habitat type. Another way to evaluate criticalness of a particular habitat would be to clarify its role as a limiting factor, or one which causes a change in population production or survival. Keith (1974) outlined criteria necessary for determining if a factor was limiting. He reported that by removing the factor of interest experimentally and observing subsequent changes in population density, relative to a control area, a factor could be considered limiting or not. This method is very similar to that outlined by White and Garrot (1991).

The purpose of this paper was to review literature pertaining to studies on the importance of mature coniferous habitat and to determine if sufficient evidence exists to conclude that this habitat type is critical to reproduction and survival of moose populations.

METHODS

To determine if there was sufficient evidence to support the hypothesis that mature coniferous forest habitat was critical to survival and reproduction of moose, we conducted a library search for journal articles concerning mature coniferous habitat and its relationship to moose thermoregulation, forage, locomotion, and predator avoidance. The criteria we used for evidence of criticalness are outlined by White and Garrot (1991). In order for a study to prove criticalness it must have excluded moose from mature coniferous habitat and monitored survival and reproduction. If moose populations decreased due to exposure, malnutrition, or predation because moose were not allowed access to mature coniferous forest habitat then this habitat type would be considered critical habitat.

IMPORTANCE OF MATURE CONIFEROUS HABITAT

Mature coniferous habitat can be important to moose populations for several reasons. It may provide cover from wind and extreme temperatures that occur during winter and summer. This cover also provides an area of shallow snow accumulation which in turn influences both forage availability of the area and aids in predator avoidance. Moose may utilize this habitat type for one or all of these reasons. The benefits gained from the utilization of this habitat type may be critical to the survival and reproduction of moose populations. However, healthy moose populations exist in areas where no coniferous cover occurs (e.g., Seward Peninsula and north slope of Alaska) (Machida 1995). If this habitat type is critical to survival and reproduction of moose then how do these particular populations persist?

Snow

In order to understand the reasons why moose select mature coniferous habitat it appears important to outline the possible causes of habitat selection. The main use of mature coniferous habitat occurs during winter. Accumulation of snow during winter and attempts to avoid deep snow by selecting dense mature coniferous habitat may be one cause for selection of this habitat type.

The selection of mature coniferous habitat in relation to snow conditions has been reported by Nasimovitch (1955), DesMeules (1964), Telfer (1970), Berg (1971), Peek (1971; 1974) VanBallenberge and Peek (1971), Berg and Phillips (1974), Brassard *et al.* (1974), Peterson and Allen (1974), Peek *et al.* (1976), Rolley and Keith (1980), Thompson and Vukelich (1981), and Ballard *et al.* (1991). All indicated increased use of, and movement into, dense cover with increases in snow depth and hardness of snow.

Thompson and Vukelich (1981) reported an increasing confinement and selection for cover of mature coniferous habitat with increasing snow depth. Cows with calves moved significantly ($P < 0.05$) shorter distances from shelter following 65 cm of snow than when snow depths were < 65 cm. This finding suggested a higher preference for cover as snow accumulated.

Schwab and Pitt (1991) reported no relationship between snow depths > 90 cm and moose selection of canopy cover types in British Columbia in mid to late winter. However, snow depth contributed to canopy cover selection in early winter. They attempted to assess the relative contributions of forage, snow depth, and heat stress to moose selection of canopy types and concluded that moose most often selected ($P < 0.10$) second growth coniferous cover with 36% crown closure, followed by mature coniferous forest with 77% crown closure.

Telfer (1970) reported that during January moose used dense coniferous and mixed-wood types significantly ($P < 0.05$) less than would be expected . Although snow depths were less in the coniferous and mixed-wood types ($\overline{X}$ = 29 cm) than in other vegetation types ($\overline{X}$ = 38 cm) differences were not significant ($P > 0.05$). By late March moose exhibited different selection patterns and used dense coniferous types significantly ($P < 0.05$) more than expected. This was attributed to increasing snow depths.

Peek (1971) and Peterson (1977) indicated that cows with calves used heavier cover than other moose during winter because calves were more impeded than older animals (Pulliainen 1974; Peterson and Allen 1974). From this it was concluded that cover was more important to calves than other moose age classes for longer periods during winter (Thompson and Vukelich 1981).

Selection of coniferous cover types as bedding sites has been suggested as an important component of winter range (McNicol and Gilbert 1978, DesMeules 1964). Minzey and Robinson (1991) indicated that moose in Michigan used conifer bed sites from early to late winter. Cows and calves were located bedding in denser hemlock (*Tsuga* sp.) stands mainly because calves needed shallower snow (Peek 1971) in order to avoid wolf (*Canis lupus*) predation (Peterson 1977, Thompson and Vukelich 1981) (see Predator Avoidance section). Bull bedding sites were found in less dense Balsam fir (*Abies balsamea*) due to reduced snow and enhanced browse appeal (Franzmann 1978).

As indicated above, there is evidence that moose select mature coniferous habitat with increasing snow depth. Factors influencing the selection of this habitat type by moose may be related to shallower snow depths, movement restrictions caused by deeper snow, forage availability in areas of shallower snow, and improved predator avoidance in shallower snow areas.

Movement — Selection of mature coniferous habitats as snow accumulates may be a result of movement restrictions in areas of deep snow outside cover. Moose may seek shelter in habitats which provide less restricted movements such as mature coniferous habitat. Moose population dynamics are assumed to be constrained by metabolized energy (Belovsky 1978). Selection of habitat types, movement patterns, and behaviour can be influenced by factors which affect the gain or expenditure of energy. Selection of mature coniferous forest habitat in winter has been thought to reflect a behavioural adaptation to avoid deep snow and thus reduce the cost of locomotion (Belovsky 1978). Nasimovitch (1955) noted that moose on the Kola peninsula in Russia, were unaffected by snow depths of 40-50 cm, while movement was impeded by depths of 60-70 cm. Snow depths of 90-100 cm were considered critical. Kelsall (1969) also reports that in eastern Canada unrestricted movements occurred at 44 cm, but movements were severely restricted when depths ranged from 70 to 90 cm. Snow depths > 90 cm were consider critical for moose survival. Coady (1974) summarized Alaska observations and concluded there was no restriction of movement when snow depths < 40 cm, slight restriction when snow depths ranged from 40 to 70 cm, definite impediments when snow depths were > 70 cm, and at depths > 90 cm movement was greatly restricted and adequate food intake was impossible.

The above studies suggest that snow depths >90 cm may be a significant limiting factor which could lead to changes in population survival. When these conditions occur greater survival should occur in areas where snow depths are shallower. One such place would be in mature coniferous habitat which reduces snow accumulation (Allen *et al.* 1987). Ballard *et al.* (1991) found that starvation was a significant cause of calf mortality during winter. The number of deaths increased with the severity of winter. Thompson and Vukelich (1981) reported that moose become confined to conifer stands when snow depths were > 90 cm. In general, this confinement represents preference but not criticalness.

Restricted locomotion as snow depths increase, and attempts to avoid deep snow conditions are one explanation for moose migrations. Ballard *et al.* (1991) identified three periods of moose migration. Autumn migration occurred between October and January and may have been influenced by winter severity. Moose were found to use different areas based on snow depths. Nasimovitch (1955) reported that migration in the Soviet Union did not occur when snow depths were < 50 cm and of short duration. When snow depths were > 70 cm and persisted there were seasonal movements from areas of deep snow to areas of less snow. Reviewed literature on moose migrations in Scandinavia by Pulliainen(1974) indicated that movement from high elevation to low elevation was closely correlated with snow conditions. Similar findings in North America by Edwards and Ritcey (1956), Knowlton (1960), Ritcey (1967), Houston (1968), and Van-Ballenberghe and Peek (1971) have demonstrated that annual migrations between distinct summer and winter ranges do occur, with the triggering mechanism being snow accumulation.

The above described migration pattern suggests that moose prefer areas with shallower snow depths such as those found at lower elevations under dense canopy. Preference may be the result of a lower cost of locomotion, increased forage, predator avoidance, or some combination which mature coniferous habitat may provide (Kelsall and Telfer 1974, Peterson 1977, Ballard *et al.* 1991). However, Kelsall and Prescott (1971), and Telfer (1967) in the Maritime Provinces noted that when moose and deer (*Odocoilieus* sp.) range overlapped at 200 m elevation moose did not migrate when snow depths ranged from 80 to 90 cm even though snow depths were more favourable and browse more abundant at the lower elevations. This suggests that moose can also tolerate deep snow under certain conditions, although the possibility exists that there may have been higher mortality because they didn't move.

The migration of moose from areas of deep snow to areas of lesser snow depths may be the result of higher browse availability (see Forage section), lower locomotion costs, or both. Selection of mature coniferous habitat may also occur for those reasons. However, evidence that movement restrictions due to the lack of mature coniferous habitat have resulted in a reduction in moose population survival has not been reported.

Forage.— Mature coniferous habitat may be critical in providing moose with access to the forage necessary to survive. The importance may lie in the decreased snow depths under these canopy types and the increased availability of forage in this area. If this habitat type was critical for moose survival and reproduction then manipulative studies which remove, or limit access to, this habitat type and monitor the moose population for increases in starvation would have to be conducted.

Brunsyk and Gilbert (1983) compared usage of stands between natural sites, which were bands of uncut timber extending from the lake shore at least 300 m, reserve sites, which were bands of uncut timber with widths of about 60 m from the lake shore, and cut stand types of coniferous species. The natural areas had the greatest basal areas of stems, and the cut areas had the smallest basal area values and lowest tree densities. Natural sites contained 41.0% more browse species than cut areas and 25.0% more than reserves. Moose showed a distinct preference for the reserve type over natural and cut areas during winter. Preferential use of reserves by moose was correlated with the proximity of adequate coniferous cover and an abundant source of browse. Although natural stands had higher overall densities and basal areas of coniferous and deciduous stems than the reserves, a tendency for a more uniform distribution of mature coniferous trees resulted in a greater interspersion of available conifer cover.

Peek *et al.* (1976) reported that when population densities, production, and survival rates of moose were compared in conjunction with forage utilization and condition it was apparent that late winter forage supplies were not the most important limiting factor to this population. They found that open cover types used in late autumn, early winter, and again in the spring were the major habitats sustaining the population. Ballard *et al.* (1991) found that, even though higher upland sites contained the highest quantity of browse, lower elevation sites were selected more frequently by moose. They attributed this to the fact that browse was more available in the shallower snow of the lower elevation sites, despite the fact that these sites had lower overall browse production. This indicates the effect that deep snow can have on browse availability and, ultimately moose selection of habitats. However, although these studies provide information on habitat use and preference, conclusions on the criticalness of conifer cover with respect to forage cannot be made.

Thermoregulation

Studies on thermal regulation of moose consider the protection from extremes of heat and cold provided by mature coniferous cover. The insulating effects from wind and radiant energy could be the reason that moose utilize this habitat type. Moen (1973) concluded that reduction of wind velocity was one of the most significant benefits of cover to animals in winter. If mature coniferous habitats were critical in moderating temperatures then the absence of it would result in changes in the rates of moose survival and reproduction. The question which needs to be answered is whether individual moose will die from exposure if they are not permitted to use the cover provided by mature coniferous habitat, and what effect these deaths would have at the population level.

McNicol and Gilbert (1978) examined the late winter bedding practices of moose in mixed upland cut-overs. The average snowfall for the winter was 61.0 cm. Approximately 81.0% of the moose beds were located in association with immature coniferous clumps. The data indicated that moose bed in a manner that allows them to utilize radiant energy from the sun. It appears that the residual coniferous cover may be an important component of moose winter range, as it provides thermal advantages to the animals. DesMeules (1964) reported that the lack of suitable bedding sites may temporarily limit utilization of winter range.

Several authors have identified cold stress as a causal factor for moose seeking shelter during winter (Van Ballenbenberge and Peek 1971; Telfer 1978; Brunsyk and Gilbert 1983). Renecker and Hudson (1986) disagreed with this idea stating that moose were more likely to suffer from heat stress in winter than cold. They found that moose are very tolerant of cold, having no respiratory increase at -30°C . Moose calves did not increase energy expenditure of thermal regulation until - 20°C, although temperatures may often be below this value.. They identified critical temperatures for heat stress in summer as being in the 14-20°C range, above these temperatures metabolic rates increased. Critical temperatures for winter were above - 5.1°C, the temperature at which the moose metabolic rates increase and thermal panting begins.

The factors affecting the biogeographical distribution of moose have been identified as food supply, climate, and habitat composition (Kelsall and Telfer 1974). The results of research by Renecker and Hudson (1986) emphasize the importance of climate and its effect on moose. Although moose seem adapted to cold temperatures, they appear to be intolerant of heat. In addition to increasing metabolism, heart rate, and respiratory rates, excessive heat causes reduced food intake and moose subsequently loose body weight during warm summer periods. Jackson *et al.* (1991) indicated that cool, dense lowland conifer stands, in combination with high quality forage, aquatic feeding areas, and adequate sources of water provide moose with preferred summer habitat. This may indicate the importance of mature coniferous habitat as thermal cover during summer and during warm periods in winter but it does not prove that the absence of this cover limits the population.

Predator Avoidance

Mature coniferous habitat may be important to moose because it provides cover which improves predator avoidance. During periods of snow accumulation, the shallower snow depths under this canopy allow better movement, thus improving escape mobility. If this habitat type was critical because it increases predator avoidance, then evidence for criticalness would have to come from manipulative studies which remove this habitat type and monitor moose survival and reproduction. If increased predation due to the lack of mature coniferous cover decreased survival and reproduction, then this habitat type could be considered critical.

The role of mature coniferous habitat in providing cover from predation to moose has not been adequately explored in the literature. The effect of predation on population dynamics of ungulates continues to be a topic of considerable debate (Boutin 1992). Predation is described as being a regulating factor in North American ungulates (Messier and Crête 1985, Van Ballenberghe 1987, Ballard *et al.* 1991), the limiting factor (Bergerud *et al.* 1983), and as exerting a significant element of control (Keith 1974). Sinclair (1989) argued that the evidence that predation operated as a regulatory factor was weak. Mech *et al.* (1987) stated that the role of wolves was secondary to moose-vegetation or moose-weather interactions.

Fuller and Keith (1980), Begerud *et al.* (1983), and Messier and Crête (1985) all concluded that wolf predation was the major limiting factor to moose populations. Boutin (1992) argued that in these cases the loss due to other factors such as malnutrition were not considered as being a compensatory component or were not considered at all. The rate of predation was thought to be related to conditions of food shortage or the severity of winter which may make moose more vulnerable to wolf predation. The influence of coniferous habitat in providing or not providing cover was also not considered.

Snow depth has an important effect on calf vulnerability to wolf predation. When snow depth on Isle Royale exceeded 76 cm, the percentage of calves in the wolf kill increased (Peterson 1977). During severe winters calf vulnerability increased and calf numbers were reduced by malnutrition. The questions we must ask are: Does increased snow depth decrease browse availability and does this cause malnutrition and an increase in wolf predation? Does increased snow impede locomotion to the point where vulnerability is increased? Finally, how does the absence or presence of mature coniferous habitat affect browse availability and locomotion to the point of affecting moose vulnerability to predation?

Bergerud *et al.* (1983) reported that weather-food interactions were not the limiting factor for moose; in the absence of wolves, availability of food has no impact on altering the vulnerability of new cohorts to predation. Peterson (1977) argued that snow conditions on Isle Royale affected the vulnerability of calves in winter to predation and malnutrition. Begerud *et al.* (1983) reported that if snow depths were a major factor influencing vulnerability, then Peterson's (1987) snow index and percent calves in the wolf kill (Allen 1979) should have been correlated but they were not (r = 0.3886, N = 16). Begerud *et al.* (1983) also found no relationship between vulnerability of calves to predation and snow conditions faced by dams in gestation (Peterson 1977). There was no correlation between calves in the wolf winter kill and the winter snow index of the year prior (r = 0.1652, N = 16).

In comparing two studies, one by Peterson (1977) on Isle Royale and the other by Begerud *et al.* (1983) in the Pukaskwa Park, the question stated by Begerud *et al.* (1983) was if both populations are limited by predation why were the two populations at such different densities (Pukaskwa, 0.2-0.4 moose/km^2 and Isle Royale, 1.1-3.0 moose/km^2)? Both exhibit similar demographic parameters, but the adaptive tactics of individuals in each population to persist must vary in response to the environment. The availability of escape habitat from wolves, (i.e. mature coniferous forest habitat), should influence the stability junction of recruitment and mortality and therefore population densities. No studies have been done linking the recruitment and mortality of a moose population to the amount of escape cover, which would prove its criticalness to the survival of the population.

Interaction and Geographic Effects

Discussions concerning the evidence of the criticalness of conifer cover have been presented under headings which relate to singular hypotheses (e.g., Snow, Predator Avoidance). However, we acknowledge that in most sections, it is the interaction effects which are being reported by the research/literature, and the critical nature of mature coniferous cover may only be evident through these interactions (e.g., predation under deep snow conditions which reduces browse availability). However, the same rigorous standards for evaluating criticalness of habitat (White and Garrott 1990) would still be needed to provide evidence for interactions.

It is also possible that the importance of geographic factors may mitigate the need for conifer in some geographic areas. In some areas, interactions which could lead to increased mortality may not occur. For example, "arctic" moose may live in areas with lower predator densities or are subjected to only seasonal predation, and may use river valleys to avoid the combined effects of wind plus cold. Under these conditions, conifer cover would not appear to be important, but its criticalness remains untested.

CONCLUSIONS

Selection of mature conifer habitat types either as a snow avoidance adaptation, to find available forage, for thermal cover, or as a predator avoidance strategy reflect preference for the cover type, but not evidence for criticalness. The studies we reviewed all indicated preference for the habitat type, however, preference is not proof of criticalness. Studies which remove the mature coniferous habitat from a moose population and then monitor their survival and reproduction are lacking. If this habitat type were removed what would be the impact on the population? Would the loss of available forage that the habitat type provides lead to malnutrition, which may increase vulnerability to predation? Would the loss of thermal cover lead to death caused by exposure? The question is that of the link between mature coniferous habitat and moose survival, and the aspects of moose life history strategies which would be lost if this habitat were removed.

Mature coniferous habitat may be an important factor in the life history of moose in certain geographic areas. It provides a habitat where moose can escape the accumulation of deep snow and the effects that deep snow have on the moose population. Deep snow can reduce the availability of forage, yet mature coniferous habitat provides an area of lower snow accumulation and thus increased forage, as compared to areas with less cover. If mature coniferous habitat is critical to moose survival and reproduction then the removal of this habitat type, or the exclusion of moose from it, would lead to a decrease in moose densities due to lower forage availability and malnutrition.

Malnutrition may have a link with increasing moose vulnerability to predation. Also, increased vulnerability may result from increased snow depths restricting movement. Mature coniferous habitat has a role in decreasing snow depths and allowing unrestricted movement. This may play an important role in providing moose with escape cover from predation. Thus, removal of this habitat type would reduce survival if it increased moose vulnerability and predation.

Mature coniferous habitat also plays a role in moose thermoregulation. Canopy cover provides shelter from wind and radiant energy. Critical temperatures for moose have been identified and moose may die as a result of overheating during winter. Also, critical temperatures for summer have also been identified and this habitat type is important in reducing heat stress during this season (Jackson *et al.* 1991). If mature coniferous habitat were critical, the removal of it and its cover would result in decreased survival and reproduction due to energy expenditure of thermal regulation.

The studies which look at the role of mature coniferous habitat in the life history of moose deal mainly with correlations between moose locations and availability of habitat in specific geographic areas. There is evidence that moose use mature coniferous habitat types to fulfil their cover and forage requirements. However, there have been no manipulation studies as recommended by White and Garrot (1991) where moose are kept out of this habitat type or the habitat type is removed, and survival and reproduction monitored. Thus, preference for these sites has been proven, but the criticalness of mature coniferous habitat in limiting moose survival and reproduction has not.

ACKNOWLEDGEMENTS

We thank Kathy Knox for assistance in gathering information and for critically reviewing the manuscript. We appreciate the constructive criticism provided by V. Crichton and two anonymous referees.

REFERENCES

ALLEN, D.L. 1979. The wolves of Minog. Houghton Mifflin Co., Boston, Mass. 499pp.

ALLEN, A.W., P.A. JORDAN, and J.W. TERRELL. 1987. Habitat suitability index models; moose, Lake Superior region. U.S. Fish and Wildl. Serv. Biol. Rep. 82(10.155) 47pp.

BALLARD, W.B., J.S. WHITMAN, and D.J.REED. 1991. Population dynamics of moose in south-central Alaska. Wildl. Mono. 114. 49pp.

BELOVSKY, G.E. 1978. Diet optimization in a generalist herbivore: the moose. Theor. Popul. Biol. 14:105-134.

BERG, W.E. 1971. Habitat use, movements and activity patterns of moose in northwestern Minnesota. M.S. thesis, Univ. Minnesota, Minneapolis.

_______, and R.L. PHILLIPS. 1974. Habitat use by moose in Northwestern Minnesota with reference to other heavily willowed areas. Naturaliste can. 101:101-116.

BERGERUD, A.T., W. WYETT, and J.B. SNIDER. 1983. The role of wolf predation in limiting a moose population. J. Wildl. Manage. 47:977-988.

BOUTIN, S. 1992. Predation and moose population dynamics: a critique. J. Wildl. Manage. 56:116-127.

BRASSARD, J.M., E.AUDY, M.CRÊTE and

P.GRENIER. 1974. Distribution and winter habitat of moose in Quebec. Naturaliste can. 101:67-80.

BRUSNYK, L.M., and F. F. GILBERT. 1983. Use of shoreline timber reserves by moose. J. Wildl. Manage. 47:673-685.

COADY, J.W. 1974. Influence of snow on behaviour of moose. Naturaliste can. 101:417-436.

DESMEULES, P. 1964. The influence of snow on the behaviour of moose. Trans. of N.E. Wildl. Conf., Hartford, Conn. 30pp.

EDWARDS, R.Y., and R.W. RITCEY. 1956. The migrations of a moose herd. J. Mammal. 37:486-494.

FRANZMANN, A.W. 1978. Moose. Pages 67-81 *in* Schmidt, J.L. and D.L. Gilbert, (eds.) Big Game of North America, Ecology and Management. Stackpole, Harrisburg, Pa.

FULLER, T.K., and L.B. KEITH. 1980. Wolf population dynamics and prey relationships in northeastern Alberta. J. Wildl. Manage. 44:583-602.

HOUSTON, D.B. 1968. The shiras moose in Jackson Hole, Wyoming. Tech. Bull. Grand Teton Nat. Hist. Ass. No. 1. 110pp.

JACKSON, G.L., G.D. RACEY, J.G. McNICOL and L.A. GODWIN. 1991. Moose habitat interpretation in Ontario. Ont. Min. Nat. Resour., NWOFTDU Tech. Rep. 52, 74 pp.

KEITH, L.B. 1974. Some features of population dynamics in mammals. Proc. Int. Congr. Game. Biol. 11:17-58.

KELSALL, J.P. 1969. Structural adaptations of moose and deer for snow. J. Mammal. 50:302-310.

_______, and W. PRESCOTT. 1971. Moose and deer behaviour in snow in Fundy National Park, New Brunswick. Can. Wildl. Serv. Rep. Ser. No. 15. 25pp.

_______, and E.S. TELFER. 1974. Biogeography of moose with particular reference to western North America. Naturaliste can. 101:117-130.

KNOWLTON, F.F. 1960. Food habits, movements and populations of moose in the Gravelly Mountains, Montana. J. Wild. Manage. 24:162-170.

MACHIDA, S. 1995. Western Alaska moose population management. *in* M. V. Hicks (ed.) Moose: Federal Aid in Wildlife Restoration Annual Performance Report of Survey-Inventory Activities, 1 July 1994-30 June 1995. Alaska Dep. of Fish and Game, Div. Of Wildlife Cons., Juneau, AK. 47pp.

McNICOL, J.G., and F.F. GILBERT. 1978. Late winter bedding practices of moose in mixed upland cutovers. Can. Field-Nat. 92:189-192.

MECH, L.D., R.E. McROBERTS, R.O. PETERSON, and R.E. PAGE. 1987. Relationship of deer and moose populations to previous winter's snow. J. Animal Ecol. 56:615-657.

MESSIER, F., and M. CRÊTE. 1985. Moose-wolf dynamics and the natural regulation of moose populations. Oecologia 65:44-50.

MINZEY, T.R., and W.L. ROBINSON. 1991. Characteristics of winter bed sites of moose in Michigan. Alces 27:150-160.

MOEN, A. N. 1973. Wildlife Ecology. W.H. Freeman and Co. San Francisco. 458pp.

NASIMOVITCH, A.A. 1955. The role of snow cover conditions in the life of ungulates in the U.S.S.R. Akademiya Nauk SSSR, Moscow (Can. Wildl. Serv. TR-RUS. No. 58).

ONTARIO MINISTRY OF NATURAL RESOURCES. 1988. Timber Management Guidelines for the Provision of Moose Habitat. Ont. Min. Nat. Resour., Wildl. Br., Toronto ON. 33pp.

PEEK, J.M. 1971. Moose-snow relationships in northeastern Minnesota. Pages 39-45 *in* A.O. Haugen (ed). Proc. Symp. Snow and Ice in Relation to Wildlife and Recreation. Iowa State Univ., Ames.

———. 1974. Initial response of moose to a wildfire in northeastern Minnesota. Am. Midl. Nat. 91:435-438.

———, K.L. URUCH, and R.J. MACKIE. 1976. Moose habitat selection and relationships to forest management in northeastern Minnesota. Wildl. Mono. 48. 65pp.

PETERSON, R.O. 1977. Wolf ecology and prey relationships on Isle Royale. U.S. Dep. Inter., Natl. Park Serv., Fauna Ser. 11. 210pp.

———, and D.L. ALLEN. 1974. Snow conditions as a parameter in moose-wolf relationships. Naturaliste can. 101:481-492.

PULLIAINEN, E. 1974. Seasonal movements of moose in Europe. Naturaliste can. 101:379-392.

RECKNER, L.A., and R.J. HUDSON. 1986. Seasonal energy expenditures and thermoregulatory responses of moose. Can. J. Zool. 64:322-327.

RITCEY, R.W. 1967. Ecology of moose winter range in Wells Gray Park, British Columbia. Proc. 4th Wksp. on Moose Res. Mgmt., Edmonton. 15pp.

ROLLEY, R.E., and L.B. KEITH. 1980. Moose population dynamics and winter habitat use at Rochester, Alberta. Can. Field-Nat. 94:8-18.

SCHWAB, F.E., and M.D. PITT. 1991. Moose selection of canopy cover types related to operative temperature, forage, and snow depth. Can. J. Zool. 69:3071-3077.

SINCLAIR, A.R. 1989. Population regulation in animals. Pages 197-241 *in* J. M. Cherrett (ed) Ecological Concepts: The Contribution of Ecology to an Understanding of the Natural World. Blackwell Scientific Publications, Oxford.

TELFER, E.S. 1967. Comparison of moose and deer winter range in Nova Scotia. J. Wildl. Manage. 31:418-425.

———. 1970. Winter habitat selection by moose and white-tailed deer. J. Wildl. Manage. 34:553-559.

———. 1978. Habitat requirements of moose - the principle taiga range animal. Pages 462-465 *in* D.N. Hyder (ed.) Proceedings of the First International Rangeland Congress. Denver, Colorado, Aug. 14-18, 1978. Society for Range Management, Denver.

THOMPSON, I.D., and M.F. VUKELICH. 1981. Use of logged habitats in winter by moose cows with calves in northeastern Ontario. Can. J. Zool. 59:2103-2114.

VANBALLENBERGHE, V. 1987. Effects of predation on moose numbers: a review of recent North American studies. Swedish Wildl. Res. Suppl. 1:431-460.

———, and J.M. PEEK. 1971. Radiotelemetry studies of moose in northeastern Minnesota. J. Wildl. Manage. 35:63-71.

WHITE, G.C., and R.A. GARROT. 1990. Analysis of Wildlife Radio-Tracking Data. Academic Press, Inc. Toronto. 183pp.