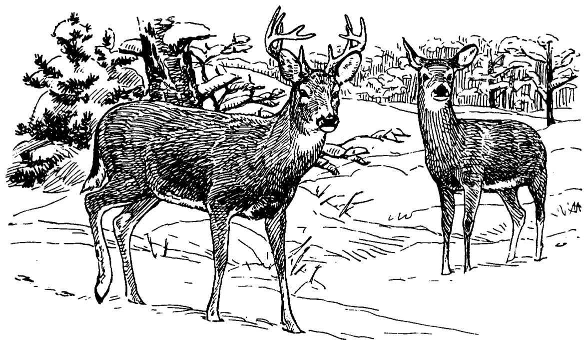
A Critical Analysis of the Winter Ecology of White-tailed Deer & Management of Spruce-Fir Deer Wintering Areas with Reference to Northern Maine



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EXECUTIVE SUMMARY

The winter survival of white-tailed deer (*Odocoileus virginianus*) is related directly to occupation of deer wintering areas (DWA) at the northern extent of their range where snow depth limits mobility and forage resources. While the specific composition of DWAs varies across the northern range of white-tailed deer, all are comprised of two basic habitat components; mature conifer stands which provide deer cover and improve their mobility, and other forest or non-forest habitats that provide deer with forage. Winter mortality is an annual event, even in average winters, because population size and density, adequacy of a DWA, predation risk, and local conditions vary. Management of DWAs is usually grounded in habitat protection that requires balancing a deer population with availability and condition of DWAs. However, typical mature spruce-fir stands operating as DWAs are not static, typically "breakdown" over time, and require constant management for both wood production and integrity as a perpetual DWA. Management of deer populations and DWAs on commercial forestland presents a unique situation of balancing a high-profile, valuable public resource (deer) critically dependent upon specialized forest habitat, with the need to effectively manage that forest habitat for its economic value. Considerable variation exists in productivity and management of spruce-fir forests, deer management goals, societal input and values, biological influences on deer and spruce-fir forests, and other human impacts where DWAs exist.

This document provides an analysis of the current knowledge of the winter ecology of white-tailed deer and management of spruce-fir DWAs that is essential to guide deer and DWA management, and to identify knowledge gaps and confounding factors that will influence future management and research decisions associated with both in northern Maine. Of particular consequence in Maine are the relationships between and among increased public concern with depressed deer populations in northern Maine, aging of regulated DWAs and LURC zoning, and trends in forest harvesting and ownership. The following highlights 15 major points, questions, and recommendations contained within the document. Readers should refer to Chapters I-IV for background information and Chapter V for an expanded summary and recommendations.

1. All deer occupying a deer wintering area (DWA) will experience a negative energy balance or weight loss because winter forage of deer is of moderate-low quality from a nutritional standpoint. Forage availability and intake are of most importance from the standpoint of energy balance, however, nutritional value and intake rate tend to decline throughout winter as deer remove the current annual growth (CAG) of most browse, and increasing snow depth reduces access to forage. Because intake rate is directly related to digestibility of the diet, providing high forage diversity and availability in DWAs helps maintain high intake rate.

2. The seasonal fat cycle in adult does is their primary physiological adaptation to withstand extended periods of limited forage availability in winter. Body fat accounts for 35-50% and 10-25% of the daily energy expenditure (DEE) of adult does and fawns, respectively, during a 90-100 day period of confinement in a DWA. Because the reciprocal proportions are met by forage consumption, reduced forage intake increases the contribution of fat to the DEE. Therefore, on a relative scale, survival of adult does is most influenced by length of winter, whereas survival of fawns is most dependent upon constant forage intake.

3. The average DEE of deer is considered low and similar to their maintenance energy requirements (1.6-1.8 x FMR) indicating that energy conservation is their principal survival strategy. Measurements of DEE and energy balance models indicate that deer mortality should be expected when severe winter conditions extend beyond 90-100 days. Fawns experience earlier and higher mortality than adult deer because, on a relative basis, they have higher DEE and less body fat and access to forage due to their age and size. Because fat reserves and body condition are best maintained through high metabolizable energy intake (MEI), maximizing browse availability and enhancing mobility to improve access to browse should be promoted in DWA management.

4. Winter mortality of deer is both density-dependent due to forage competition caused by high population density in a confined area with limited resources, and density-independent from predation by coyotes. However, both sources of mortality are largely

dictated by winter severity, principally snow depth that affects forage availability and mobility of deer, and their abundance, distribution, and relative vulnerability to predation. Coyotes predate all sex/age classes of deer, but fawns are most vulnerable, and predation is greatest when forage competition and malnutrition occur in late winter. Thus, the probability of additive mortality from predation is influenced by winter conditions that exacerbate all mortality factors, indicating the value in managing DWAs for high browse availability and mobility of deer.

5. Well-established coyote populations in Maine should be considered a permanent source of winter mortality that has effectively lowered the carrying capacity where deer are confined to DWAs for extended periods. Historic population goals established during periods of coyote-free DWAs are likely not attainable and deer population goals need to reflect coyote predation during winter. Coyote predation should be considered a limiting not regulatory factor of deer populations because depressed regional deer populations in Quebec have recovered after a series of mild winters, arguably the most influential factor, in combination with habitat restoration and coyote population control.

6. Deer typically have reduced productivity after severe winters because of high mortality and reduced body condition of does that affect fecundity and fawn survival. The impact of a severe winter can have a lagged, 2-3 year effect, and a series of consecutive severe winters that continually depress productivity and enhance predation can produce regional population decline. Conversely, a series of mild winters is probably required to grow a depressed deer population at its northern extent through reduced mortality from malnutrition and predation, and higher productivity through improved nutritional status and body condition of yearling and adult does. The potential impact of severe winters on northern deer populations is best addressed by maintaining large DWAs that provide optimal cover, forage, and deer density.

7. The disproportionate importance of DWAs is evident by the fact that DWAs generally represent only 5-15% of the annual range. However, deer display very strong fidelity to their DWA and are very reluctant to abandon it. This has several implications to DWA management including 1) maintenance and habitat improvement should focus on DWAs

currently used by deer, 2) colonization of a DWA where deer are removed (e.g., predation, severe winter) will probably not be immediate, and 3) what happens to deer when their DWA is removed is unknown, and 4) it is also unknown how deer colonize new DWAs in a landscape that has been heavily fragmented by timber harvesting. Research designed to investigate such topics is warranted in Maine if increasing the northern deer population is a management goal in face of reduced mature spruce-fir habitat, and a trend toward shorter rotation age in spruce-fir habitat that is in decline. This research would likely require considerable investment in radio-collared deer for at least 5 years, and should include aspects that investigate annual mortality factors and movement through and occupation of habitats within a landscape perspective.

8. Snow depth, usually ≥30 cm, is the main factor that triggers deer to occupy DWAs; deer become confined to dense conifer stands when snow depth exceeds 40-50 cm. The use of a DWA expands and contracts as snow and sinking depth influence deer mobility. All DWAs are comprised of two basic habitat components; mature conifer stands that provide deer shelter and improve their mobility, and other forest or non-forest habitats that provide forage. The best DWAs contain high interspersion of cover and food that provide deer access to resources throughout winter under a wide range of snow conditions.

9. The best winter cover for deer is provided by mature forest stands that are comprised of at least 50% conifers with 50% crown closure, and at least 10 m tall. Although exactly how much conifer cover deer require is unknown, where snow depth regularly exceeds 50 cm, deer may require conifer stands with at least 70% crown closure, and where snow depths rarely exceed 20 cm, 30% conifer cover may be adequate. DWAs >100 ha should be the focus of management and conservation efforts.

10. Extensive commercial clear-cutting that removes softwood and creates abundant browse reduces the carrying capacity of deer winter habitat in northern Maine. Silvicultural techniques to manage spruce-fir timber can be identical to those used to create ideal DWA conditions. How these techniques are applied to accomplish both goals

on the same property will require creativity and compromise on the part of both the landowner and any regulatory agency. Three main objectives should be considered when creating and maintaining an ideal DWA including:

1) maintain an adequate amount of functional cover at all times,

2) perpetuate a constant, abundant supply of accessible forage, and

3) maintain a high level of interspersion and mobility that provides functional cover and accessible food.

11. Maintenance of DWAs on commercial timberland requires a conscious effort on the part of the landowner to identify areas where mature spruce-fir stands can be developed and perpetuated. Timber harvesting can and should be used to shift the location of these stands over time to ensure they don't become over-mature and lose their ability to provide cover for deer. In some situations, timber harvesting may need to be deferred in order to develop and maintain mature conifer cover. Establishing minimum cover requirements based on annual winter severity will help ensure adequate cover is maintained to meet DWA objectives, while minimizing the burden to private landowners.

12. A winter severity index (WSI) that uses a combination of measurements of snow depth, sinking depth, and ambient temperature reflects the direct relationship between winter severity and the body condition, productivity, and mortality of wintering deer, and is probably the most useful tool that deer managers have to adapt and adjust annual harvest goals to address long-term deer population goals. The use of a WSI offers many advantages including annual assessments and management responses, as well as long-term data sets that should identify changes associated with climate change. These data are valuable for analyses of weather and herd response, temporal evaluation of a DWA as it ages or is harvested, and to compare biological and economic value of a DWA.

13. A long-term evaluation of the number of days with 50 cm snow depth and/or relative WSI scores could be useful to produce a stratified, landscape approach in managing DWAs in Maine. One possible approach is to establish habitat management zones based

on differences in average winter severity and corresponding criteria for minimum crown closure (e.g., 70% in north, 50% in central, 30% in south).

14. Land use zoning through the Land Use Regulation Commission (LURC) restricts timber harvesting in an effort to manage and protect DWAs. However, LURC zoning is insufficient for maintaining functional DWAs long-term because it only protects the shelter portion of a DWA. LURC zoning would be more effective if it better reflected that DWAs are larger than the shelter component, and that the dynamics of forest growth and replacement of cover and forage contributes to the viability of a DWA over time. Zoning, managing, and conserving DWAs requires accurate and continuous effort in identifying use and location of DWAs, and such work is critical to help LURC be more effective.

15. The traditional "expert" or authoritative approach of management is not recommended to address the DWA issue in Maine, rather, a co-managerial approach that will require shared responsibility is advocated. Given the myriad of stakeholders and their varied knowledge and attitudes, high public value and sentiment for deer, dramatic shifts in land ownerships and turnover, economic issues, and recent history of public referendums, strong and responsible leadership by one organization is needed to implement an objective and successful human dimensions approach to address deer and DWA management in Maine.

INTRODUCTION

The winter survival of white-tailed deer (*Odocoileus virginianus*) at the northern extent of their range, as in northern Maine, is inextricably linked with the availability of adequate winter habitat in most years. Winter habitat, or deer wintering areas (DWA), generally consists of mature spruce (*Picea spp.*)-fir (*Abies balsamea*) stands in northern Maine that provide shelter from wind and reduced snow depth relative to other forest stands. Energy conservation is the overall strategy of deer during winter, and quality and quantity of DWAs influence winter survival. Winter mortality is an annual event even in average winters because of the interrelationships among, and varying conditions in deer population size and body condition, adequacy of resources within a DWA, predation by eastern coyotes (*Canis latrans*) well established in the past 30 years, snow depth and duration, and other weather variables.

Spruce-fir stands that serve as effective DWAs have physical characteristics that ameliorate environmental conditions outside a DWA allowing deer to conserve energy, access forage, and increase survival within a DWA. The dense conifer cover within a DWA, sometimes referred to as the core or shelter area, is often used to describe the best conditions and locations of cover in large DWAs with variable stand characteristics; usually this area has the most effective crown closure, hence largest trees. Habitual use of specific DWAs for decades is common, however, the fate of deer "losing" their DWA to timber harvest is unknown, and relates directly to forest management in DWAs given their high economic value.

The timber harvest strategy in spruce-fir stands, regardless of whether they are part of a DWA, is influenced by many factors including age, natural disturbance, disease, insects, and economics. Timber harvests in DWAs are of obvious concern to a number of stakeholders including deer managers, commercial and private landowners, hunters, outdoor recreationists, and conservation groups. Management of DWAs is usually grounded in habitat protection that requires balancing a deer population with specific habitat availability and conditions. However, mature spruce-fir stands are not static, typically “breakdown” over time, and require constant management for both wood production and integrity as a perpetual DWA.

Management of deer populations and DWAs on commercial forestland presents a unique situation of balancing a high-profile, valuable public resource (deer) critically dependent upon specialized forest habitat, with the need to effectively manage that forest habitat for its economic value. Maine has experienced three forest-wildlife public referendums in the past 25 years demonstrating the increasing and potential influence of public regulatory power in natural resource management. An improved human dimensions approach would presumably better engage the public and benefit defendable, scientific approaches to deer and DWA management.

In theory, creation of an “ideal” management strategy for DWAs and winter populations of deer should be possible given the research attention both have received due to their high societal and economic value. Ironically, these values are increasing and many stakeholders in society will continue to influence related management direction and decisions. However, it is also obvious that across the northern range of white-tailed deer considerable variation exists in productivity and management of spruce-fir forests, state and provincial deer populations and goals, societal input and values, biological influences on deer and spruce-fir forests, and other human impacts where DWAs exist. This document provides a critical analysis of the current knowledge of the winter ecology of white-tailed deer and management of spruce-fir DWA that is essential to identify knowledge gaps and confounding factors that will influence future management and research decisions associated with both in northern Maine.

CHAPTER I: BIOENERGETICS, PREDATION, WINTER SEVERITY INDEX

Food Habits

The composition, availability, and use of forage in a DWA generally reflect, in large part, the value of a DWA to body condition and winter survival of deer. It is important to recognize previous and current impacts of deer on the composition and availability of winter browse. Plant composition and forage production are not optimal in many DWAs because it is generally accepted that dense winter populations of deer severely reduce or eliminate certain browse species, both annually and long-term. Most traditional DWAs indicate such and this is neither surprising nor unexpected in a situation where forage resources are limited in face of high ungulate density.

Specifically, ground hemlock (*Taxus canadensis*) and northern white cedar (*Thuja occidentalis*) have been reduced regionally for decades (Huot et al. 1984, Mattfeld 1984). The influence of heavy, annual winter browsing coupled with timber harvests reduces northern white cedar, generally considered the most valuable coniferous cover and forage; increase in balsam fir (*Abies balsamea*)-spruce (*Picea spp.*) results (Blouch 1984). Likewise, the availability of balsam fir, the staple browse of resident deer, is now limited to blow downs due to historic over-browsing on Anticosti Island, Quebec (Sauvé and Côtè 2006 a, b), and eradication of understory balsam fir is predicted in 40-50 years (Potvin et al. 2003). Alteration of deciduous forage also occurs (Mattfeld 1984), although most studies have focused on hardwood regeneration in cutover areas not within DWAs specifically. Of additional concern is that moose can reduce available deciduous browse in clearcuts adjacent to, and probably within a DWA (Pruss and Pekins 1992).

Winter forage is principally a mix of coniferous and deciduous woody browse. Forage use in spruce-fir DWA is largely determined by forage availability that is influenced by stand condition, snow depth, and current and previous browsing pressure. Direct surveys of browse use have occurred in numerous DWAs in most state and provincial DWAs during and after winter; rumen analysis and observation of released/tractable captive deer (Crawford 1982, Shively 1989, Bock 1993, Pekins 1995) have also provided food habits information. Browse species are generally ranked by use and preference, and overall, little variation exists in the relative rank and importance of forage species across the range of spruce-fir DWA. However, preference, contribution, and importance of specific browse species within DWAs are not necessarily similar because of the influence of the aforementioned factors that influence forage composition. Further, forage use moves from selective to general as choice and availability decline as winter progresses (Brown and Doucet 1991).

Deciduous species considered important and common in the diet include beaked hazel (*Corylus cornuta*), hobblebush (*Viburnum alnifolium*), yellow (*Betula alleghaniensis*) and white birch (*B. papyrifera*), dogwoods (*Cornus spp.),* and red (*Acer rubrum*), striped (*A. pensylvanicum*), and mountain maple (*A. spicatum*); coniferous species include balsam fir, northern white cedar, hemlock (*Tsuga canadensis*), and ground hemlock (Blouch 1984, Huot et al. 1984, Mattfeld 1984, Bock 1993, Pekins 1995). Starvation foods include red and white spruce (*P. glauca*), tamarack (*Larix laricina*), alder (*Alnus incana*), and beech (*Fagus grandifolia*) (Blouch 1984, Huot et al. 1984, Mattfeld 1984, Sauvé and Côtè 2006 a, b).

The nutritional contribution and importance of litterfall in the winter diet is now well recognized (Crawford 1982, Huot 1982, Hodgman and Bowyer 1985, Ditchkoff and Bowyer 1998), but it was presumably overlooked historically because use was not easily measured in typical browse surveys. The most common lichen species used by deer include *Usnea* spp. (Voigt et al. 1997, Skinner and Telfer 1974), *Alectoria* spp. (Wetzel et al. 1975, Tremblay et al. 2005), *Evernia* spp. (Ditchkoff and Servello 1998), *Bryoria* spp. (Tremblay et al. 2005, Ward and Marcum 2005), *Nodobryoria* spp. (Ward and Marcum 2005) and those in the Genera *Ramalina* and *Lobaria* (Tremblay et al. 2005). The importance of litterfall in the winter diet can be surmised from the foraging behavior of deer on Anticosti Island that consume only 3 basic forages; balsam fir and white spruce that are rated poor relative to nutrition and preference, and litterfall (Tremblay et al. 2005, Lefort et al. 2007). Although winter mortality of fawns is high on Anticosti Island (e.g.; 37%, Taillon et al. 2006), deer continue to persist while consuming this marginal-starvation diet at the northern most extent of their range, indicating indirectly the importance of the availability and consumption of litterfall in the winter diet.

Initial reports of litterfall use were from trained, captive deer in Maine (Crawford 1982, Shively 1989) and subsequent studies suggested that not only was use of litterfall common, it contributed measurably to available digestible energy (DE), DE intake (DEI), and energy balance (Hodgeman and Bowyer 1985, Ditchkoff and Servello 1998, Tremblay et al. 2005). Lichens are higher in DE than typical winter browse species, and likely have synergistic effects in digestion, effectively raising the overall digestibility of a mixed winter diet (Rochelle 1980, Jenks and Leslie 1988, 1989, Tremblay et al. 2005). The unaccounted consumption of litterfall may help explain the difficulty predicting deer survival from nutritional measurements of browse (Gray and Servello 1995).

Importantly, the availability of litterfall, presumably pulsed by winter storms, is not affected by current or past browsing, it "reappears" at end of winter during snowmelt when deer are in poorest condition, and fawns are not disadvantaged in its consumption that increases throughout winter (Ditchkoff and Servello 1998, Tremblay et al. 2005, Taillon et al. 2006, Lefort et al. 2007). Because litterfall is a byproduct of mature softwood stands (Ditchkoff and Servello 1998, Tremblay et al. 2005), its relative availability, contribution, and importance to wintering deer will be a function of the composition and age of stands within a DWA.

Because deer realize and are adapted to a negative energy balance in winter, differential ranking and relative use of forage species among DWAs does not necessarily relate directly to differences in survival among DWAs. For example, the winter diet of the introduced deer population on Anticosti Island, Quebec consists of only balsam fir, white and black spruce (*P. mariana*), and lichens which are rated as poor-starvation foods. Although deer density has remained high for decades on this marginal diet, it is projected that it will decline with continued degradation of winter habitat and further reduction of balsam fir that has dominated the historic diet (Sauvé and Côtè 2006 a, b). The food habits of deer in DWAs are probably best considered from the standpoint of forage availability and consumption level rather than species ranking.

Nutritional Value of Winter Browse

The nutritional value of winter browse has been measured with both *in vivo* (within the animal) and *in vitro* (outside the animal) techniques. The inherent difficulty of *in vivo* studies is telling; maintenance of captive deer on strict winter browse diets for extended periods is difficult because of the low nutritional value of winter browse. Many studies have measured the nutritional value of specific browse species, although such measurements probably have limited value for assessing nutritional status because deer consume mixed diets. Large species-specific nutritional differences are evident (e.g., northern white cedar versus balsam fir; Ullrey et al. 1968), however, most browse species are considered of moderate-low nutritional value as compared to other seasonal foods. It is expected that availability and nutritional value of browse declines throughout winter as confined, high densities of deer continuously forage in a browse-limited environment (Brown and Doucet 1991). Thus, the relationship of forage nutrition to body condition has a temporal aspect related to length of winter.

The low digestibility of most browse species and the related negative effects of secondary compounds in coniferous species (Robbins 1993) are probably not realized entirely. Presumably, the synergistic effect of mixed diets and physiological adaptations of deer counteract the negative characteristics of individual browse species (Robbins 1993). It is telling that the winter diet of deer on Anticosti Island, Quebec consists of only balsam fir, white spruce, and lichens, yet deer persist (though often with high mortality) despite the poor nutritional value of this diet.

The description of the nutritional value of browse includes specific measurements used to describe and extrapolate the diet to the condition and survival of deer from the perspective of energy balance. Terms include dry matter (DM), dry matter intake (DMI), digestible dry matter (DDM), digestible energy (DE), digestible energy intake (DEI), metabolizable energy (ME), and metabolizable energy intake (MEI), fasted metabolic rate (FMR), daily energy expenditure (DEE), lower critical temperature (T_{lc}), and heat increment (H_iE); definitions are included in Table 1.

In vivo measurements of DE of coniferous browse species range from a high of 50% for northern white cedar (Ullrey et al. 1964, 1967, 1968), to 27-38% (Ullrey et al. 1968) and 49% for balsam fir (Mautz et al. 1976); the latter value was estimated from simultaneous equations of mixed ration data, not a single forage feeding trial. Spruce has not been evaluated but is considered a starvation food as deer avoid it if other browse exists; the physical characteristics and secondary compounds associated with spruce presumably deter browsing. Despite a fairly high DE value, consumption of only balsam fir resulted in death of some experimental deer (Ullrey et al. 1968), indirect evidence of the importance of consuming a mixed diet.

The DE of deciduous browse species from *in vivo* measurements ranges from 30% (aspen (*Populus termuloides*); Ullrey et al. 1964) to 55% (hobblebush); the latter value was estimated from simultaneous equations of mixed ration data (Mautz et al. 1976). The DE of deciduous browse species measured *in vitro* ranged from 42% (American beech) to 62% (paper birch) (Robbins and Moen 1975). The average DE of 5 deciduous species measured *in vivo* by Mautz et al. (1976) was 39%, whereas the average was 52% for 18 species measured *in vitro* by Robbins and Moen (1975); large discrepancies (>15%) in these studies occurred in the DE estimates of red maple and beaked hazel.

Differences in nutritional data among studies probably result, in large part, to the variability of experimental browse. For example, Gray and Servello (1995) used browse of smaller diameter than Mautz et al. (1976); smaller diameter, current annual growth (CAG) has less fiber and would be more digestible than older, larger diameter browse. Presumably, the relative nutritional value of browse declines during winter because as deer selectively consume CAG, its availability declines throughout winter. Therefore, averaging values from multiple studies to extrapolate winter DEI/MEI should be acceptable because the availability of CAG is presumably not unlimited, but a function of winter length and severity, deer density, and forage composition within a DWA.

Probably more important is that as CAG declines in the diet, fiber content would increase, and passage rate and intake rate would decline (Robbins 1993).

The ME of browse species is the difference between DE and energy losses associated with urine and gaseous products (primarily methane). Urinary losses are higher in coniferous (19% of DE) than deciduous species (11% of DE); the higher concentration of secondary compounds in conifers reduces ME because of their removal and excretion in urine. Methane loss is relatively low on browse diets, only 5% of DE. As a proportion of DE, the ME of winter browse is 76-80% of DE (Robbins 1993).

Of most practical use and value in assessing nutritional value of winter forage is the measurement of DE/ME from typical mixed diets of winter browse; two studies provide unique data from mixed diets. Mautz et al. (1976) fed 8 diets consisting of varied proportions of 3 deciduous species and 1 coniferous species (balsam fir or hemlock), and Gray and Servello (1995) fed 8 diets of varied proportions of 3 deciduous species, 1 conifer (northern white cedar), and lichen. The DE of these diets ranged from 38-43% and 42-49%, respectively. The latter study revealed that DMI and DEI were directly related; DMI increased about twofold across a 20% range of DE. However, they purposefully avoided feeding common coniferous browse species (i.e., balsam fir and hemlock) to avoid the influence of secondary compounds in the study. Regardless, in neither study did deer maintain body weight, indicating the inherent negative energy balance experienced by deer in winter, irrespective of diet.

However, because a minor increase in DDM can elevate DEI substantially (Gray & Servello 1995), habitat management for the most nutritious and digestible species and diets is not without merit. Certainly the combination of high food availability and high DMD in the diet will provide the optimal diet and intake rate for deer. Further, diets high in coniferous species should not be considered poor. Although Gray and Servello (1995) only used northern white cedar in their diets, it is the most digestible and nutritious coniferous browse (Ullrey et al. 1968), and the highest DEI was on the diet with the most

Table 1. The following terms are commonly used to describe the nutritional value of winter forages and diets, and bioenergetics of deer.

Dry matter (DM): indicates a measurement where the sample in question contains 0% water; measured by drying a sample to constant weight; provides a comparative measurement for nutritional calculations that eliminates the differences in water content among forages.

Dry matter intake (DMI): measurement of the forage intake of an animal expressed in terms of DM; average bite size, species-specific DM content of forages, and bite rate need to be known to calculate DMI.

Digestible dry matter (DDM): measurement of the digestibility of a forage/diet; calculated by measuring DMI and subtracting the amount of fecal DM; typically 35-50% for winter forages/diets.

Digestible energy (DE): measurement of the energy digested in a diet; calculated by measuring the energy content of forage and feces (DM basis), multiplying these values by DM intake and DM fecal production, and subtracting total fecal energy from total intake energy; the % DDM and % DE are nearly identical in value, and most mixed browse diets with some component of coniferous species have similar energy content.

Digestible energy intake (DEI): measurement of the DE associated with forage intake; usually calculated as daily intake by measuring DMI/24 hr and multiplying by an assumed DE value; estimating the DEI of a mixed diet usually requires using a DE value from closely related forages or diets measured previously.

Metabolizable energy (ME): measurement of the DE in a diet but more accurate and less than DE; calculated the same as DE except that the energy losses associated with urine (DM basis) and methane production during digestion (about 5% of total forage energy) are accounted for; the % ME of a winter forage/diet is about 75% of its % DE.

Table 1 (cont.).

Metabolizable energy intake (MEI): measurement of the ME associated with forage intake; usually calculated as daily intake by measuring DMI/24 hr and multiplying by an assumed ME value; it is used to compare against the maintenance (daily) metabolizable energy requirements of deer to assess energy balance.

Fasted metabolic rate (FMR): measurement of the energy expenditure of a bedded, post-absorptive, thermoneutral animal; considered a minimal baseline value to add and compare all other energy costs of life; used as a multiplier/ratio to evaluate the relative efficiency of daily energy expenditure.

Daily energy expenditure (DEE): the total energy cost associated with life including basal metabolism, thermoregulation, activity, and digestion; often described as a ratio with FMR and typically is >2.0; the FMR:DEE ratio of deer in winter is about 1.7 indicating their efficient energy conservation.

Lower critical temperature (T_{lc}): temperature below which an animal must expend extra energy to maintain body temperature; generally considered to be below the average ambient temperatures experienced by white-tailed deer in winter; thermoregulatory costs are presumed to be minimal for deer in winter.

Heat increment (H_iE): the "excess" heat produced during digestion that substitutes for heat loss/production below the T_{lc} of an animal; it effectively lowers the T_{lc} of fawns consuming browse diets about 10º C.

cedar. Likewise, the 4 highest DEI/MEI values measured by Mautz et al. (1976) were realized on diets with 30-55% balsam fir and hemlock. The ability of deer to consume and digest high volumes of coniferous species (>75%) throughout winter is evident from studies on Anticosti Island (Taillon et al. 2006). Taken collectively, the evidence indicates that although diet quality is important and measurable differences between browse species exist, total intake that is related directly to DE and forage availability is the most important factor to consider in DWA management.

Balancing winter deer populations with forage resources in a DWA is key to enhance nutritional status and survival of deer. Long-term, over population of deer in a DWA reduces forage availability, diversity, and quality (Mattfeld 1984); optimal DEI is not realized in such situations because species highest in DMD are often eliminated, and limited CAG and higher concentrations of secondary compounds and fiber that reduce DMD are characteristic of plants over-browsed annually (Robbins 1993). Although deer often persist in such situations, arguably the long-term capacity of a DWA to support deer is reduced, and high mortality usually occurs in severe winters causing dramatic population fluctuations (Mattfeld 1984). Of further consequence is that recovery of browse is slow in DWA overstocked with deer long-term.

Extrapolation of nutritional data predicts moderate-high weight loss in deer consuming singular diets of deciduous species, northern white cedar, and balsam fir (Ullrey et al. 1967, 1968), as well as mixed coniferous-deciduous diets (Mautz et al. 1976, Gray and Servello 1995), and deciduous-only mixed diets (Gray and Servello 1995). Thus, intake rate, which is presumably influenced most by forage availability, not specific forage use, is probably more important in assessing the value of a DWA and predicting deer survival. Unless forage availability is restricted to starvation foods, differences in species composition in a mixed diet probably have minor influence on the nutritional status of deer. The persistence of deer consuming poor diets on Anticosti Island is evidence of the importance of intake rate relative to the nutritional ranking of specific species. Although one would predict that survival and condition of deer would decline as the diet gradually switches to more spruce and less balsam fir, little evidence of such exists when balsam fir remained 50% of the diet (Taillon et al. 2006).

There is a strong, nearly 1:1 relationship (Y = -0.049 + 0.99X; R^2 = 0.96; Robbins 1993) between the dry matter digestibility (DMD) and the digestible energy coefficient (DE) of ruminant diets. This relationship provides a unique opportunity to estimate DE intake (DEI) from the daily fecal production of free-ranging deer. Such an approach has been used in Scandinavia by back-tracking moose in snow and collecting pellet groups along the daily track, and could possibly be used with free-ranging deer that allow close observation. After calculating the fecal DM and assuming a DMD, DEI is estimated from the 1:1 relationship of DMD:DE. An average DMD of a typical, mixed winter browse diet of deer can be calculated from past studies (e.g., 45-50%).

Energy Requirements and Expenditure

The use and value of forage nutritional data is dependent on accurate estimates of energy requirements and expenditure. Although protein has received attention relative to winter nutrition of deer, available and digestible protein in the diet is low in winter (Mautz et al. 1975). Deer cannot meet their daily protein requirements from winter browse, and actually conserve protein through effective recycling of urea during winter (Robbins et al. 1974b, Del Guidice 1987a, b, 1990 b); delayed fetal development during winter is a related evolutionary strategy (Robbins 1993, see beyond). Thus, energy is considered the best currency to assess quantitatively the nutritional status of deer, and provides a link between the forage and cover characteristics of a DWA and the winter energy balance and survival of deer (Mautz 1978).

Energy expenditure is typically measured either of three ways; via measurement of oxygen consumption, measurement of MEI, or with isotopic techniques. Energy expenditure and requirements of captive and free-ranging deer have been measured in a number of environmental conditions with these techniques, and winter energy balance has been modeled with such data. Ultimately, such data and exercises help predict the nutritional carrying capacity of a DWA in terms of animal days or length of occupation.

Such exercises also identify the relative contribution of energy inputs and costs of life processes and activities to energy balance and survival.

Fasting metabolic rate

Unfortunately, deer biologists continue to cite the Silver et al. (1969) study that suggested that deer have a reduced fasting metabolic rate (FMR) in winter as a critical physiological adaptation to conserve energy in a resource limited environment. However, there was no evidence of such in that study; the authors should have identified that the summer FMR was abnormally high, not that winter FMR was reduced. Subsequent studies verified that winter and summer FMR of deer are not different (Mautz et al. 1992, Pekins et al. 1992). It is important to note that these later studies had the advantage of measuring animal activity and manipulating experimental temperatures during metabolic measurements, whereas the pioneering efforts of Silver et al. (1969) had no such capability. Unaccounted activity and thermal stress of experimental deer produced the abnormally high FMR in summer. Of critical importance is that, absent this near "magical" survival adaptation, the role of a DWA and other physiological and behavioral adaptations of deer assume magnified importance in their winter survival.

The FMR is measured on fasted, bedded, thermoneutral deer and is considered a baseline value to compare additional energy costs associated with life functions including thermoregulation, activity, and gestation. This value can be used to evaluate the relative efficiency of the daily energy expenditure (DEE) of free-ranging animals with FMR:DEE ratios. Importantly, there was remarkable consistency in the FMR of adult female deer measured in multiple studies spanning 4 decades (Silver et al. 1969, Thompson et al. 1973, Kanter 1989, Mautz et al. 1992, Pekins et al. 1992, Pekins et al. 1998). Like most ungulates, the FMR of adult deer is higher than predicted allometrically (70 kcal/kgBW$^{0.75}$/d), averaging about 80 kcal/kgBW$^{0.75}$/d across these studies.

Of major consequence is that fawns have 11% higher FMR than adult deer (Kanter 1989, Jensen et al. 1999), typical of the difference between juveniles and adults of most species (Robbins 1993). Thus, fawns are at distinct disadvantage because DEI is typically limited in winter, and fawns have higher energy requirements than adult deer on a relative scale. The higher and earlier winter mortality of fawns than adults provides obvious evidence of such.

Thermoregulation

Winter temperatures typical of the northern range of deer are usually considered to have negative influence on their energy balance. However, measurement of the lower critical temperature (T_{lc}), that temperature below which metabolism increases to maintain body heat, indicate that fasted adult does are thermoneutral above -10° C (Mautz et al. 1985, Kanter 1989, Mautz et al. 1992) and fasted fawns above 0° C (Kanter 1989, Jensen et al. 1999). These estimates are similar to average daily high ambient temperatures in northern deer range (Huot et al. 1984, Mattfeld 1984).

Of more importance, however, is the estimate of the T_{lc} of fed deer because free-ranging deer are probably never fasted. The process of digestion elevates the metabolic rate, but the "excess" heat produced during digestion can substitute for heat loss/production below the fasted or fed T_{lc}. This is termed the heat increment of feeding (H_iE) and its effect is to effectively lower the T_{lc}. Measurements of the H_iE indicated that fawns realized about a 10° C reduction of the T_{lc} on browse diets (Jensen et al. 1999). Furthermore, the relative level of intake influenced the effect of H_iE on the T_{lc}; fawns on high browse intake realized a T_{lc} of -15° C versus -6° C for fawns on low intake. Metabolic rate increased only 15% down to -20° C; the average daily low ambient temperature averages -18° C in northern deer range (Huot et al. 1984). It was concluded that the thermoregulatory costs of free-ranging fawns consuming natural forage is probably minimal because the experimental fawns were on a poorly insulative substrate; likewise, it follows that thermoregulatory costs of adults are minimal. The substitutive thermoregulatory effect of H_iE associated with high browse intake is most important to fawns because their FMR and T_{lc} are higher than those of adult deer.

Gestation

It is generally accepted that seasonal changes in forage quantity and quality causes the restricted reproductive cycle of northern deer; breeding cycles of southern deer are less restrictive (Bronson and Heideman 1994). Many biologists have assumed that gestation influences survival of pregnant does through elevated energy costs (e.g., Moen 1976, Mautz 1978). Intuitively this is logical because northern deer breed in November and have a gestation period of 200 days encompassing winter (Haugen and Davenport 1950 and others), and malnutrition and mortality is normal in northern populations. Related evidence includes the relationship between poor winter nutrition of does and high neonatal mortality (Verme 1965, 1969, 1977). Further, birth mass of fawns is influenced by the relative nutritional plane of does; fawns of does on a high nutritional plane are much larger than those of does on a lower plane of nutrition (3.5 versus 1.9 kg; Verme and Ullrey 1984).

Although the nutritional condition of pregnant does influences productivity, they are adapted physiologically to minimize the effect of resource limitation during winter by delaying fetal development (Armstrong 1950). The physiological advantage of such is a delay in the high daily protein requirement associated with fetal development (Robbins et al. 1975, Robbins 1993). Available and digestible protein in the diet is low in winter (Mautz et al. 1975) and deer typically cannot meet their daily protein requirement (Robbins et al. 1974), hence, fetal growth would be problematic and is delayed until highly available and digestible protein occurs in spring forage.

Measurement of the energy cost of pregnant does throughout gestation provided a temporal analysis of the energy costs of gestation (Pekins et al. 1998). Energy costs associated with gestation were minimal during the first two trimesters in January-March when deer usually experience weight loss and negative energy balance. Energy costs increased exponentially the final trimester beginning April 1; 92% of the total energy cost of gestation occurred in the final trimester (Fig. 1). When compared to the date of average green-up in northern New Hampshire (April 22), 77% of the cost occurred afterward. Thus, although gestation itself is not energy costly during winter, the relative condition of pregnant does at end of winter, and particularly the length of winter and timing of spring green-up in April will strongly influence productivity.

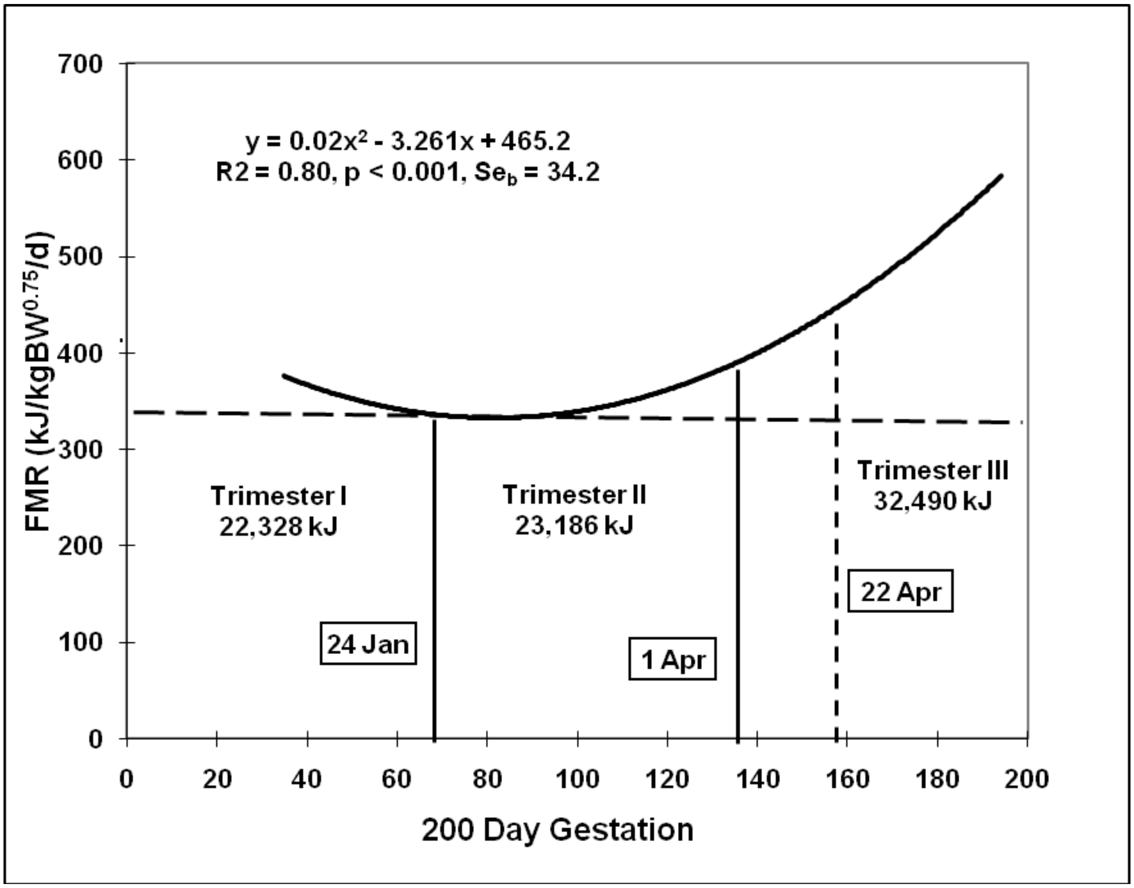

Figure 1. This figure depicts the relationships among energy cost of gestation, gestational period, winter length, and average date of spring greenup (April 22). There is minimal energy cost associated with gestation during winter. The majority (77%) of energy cost is delayed until the third trimester (after April 1) and increases exponentially thereafter. These data indicate the potential impact of extended winter conditions on pregnant does and productivity; data are from Pekins et al. (1998).

Locomotion, Mobility, and Activity

The debate as to whether deer principally occupy DWA for enhanced mobility to reduce energy expenditure associated with locomotion in deep snow, versus occupying conditions that provide critical cover and forage resources seems analogous to the question of the "chicken and the egg." Distinct separation of these factors seems illogical because occupation of a DWA is directly related to snow depth, and the relative availability of browse is indirectly related to snow depth. Dumont et al. (2005) concluded that foraging behavior in a DWA was influenced by locomotion costs in snow, and that deer adjusted their behavior and forage choices accordingly; diet quality declined as snow depth and winter increased. However, one could also conclude that deer simply react to snow depth by avoiding conditions where they are essentially immobile and forage is basically unavailable, that deer actually create conditions in DWAs where locomotion costs are negligible in their energy budget, and that the nutritional value of a browse diet declines predictably as winter progresses because forage quality and quantity are also declining.

Dumont et al. (2005) also proposed that deer have a strategy to increase retention time of the diet (low passage rate) to reduce activity when locomotion costs are high. This conclusion has little merit because retention time/passage rate is directly related to diet quality (fiber content; Robbins 1993) that is strongly influenced by snow depth and time of winter. As forage quality declines, consumption and deer activity should also decline because they cannot process as much forage. Simply put, these declines should occur at end of winter when forage quality and availability are lowest; it is not strategy, it is a consequence of predictable relationships. Further, there is no evidence that daily locomotion costs in a DWA increase throughout winter; rather, deer probably experience temporary, pulsed increases related to snowfall and subsequently eliminate them with their travel patterns.

Schmitz (1990) dismissed, in part, the validity of the energy minimization strategy proposed by early deer researchers such as Moen (1976) and Mautz (1978) because his study deer increased activity to access supplemental food and incurred benefit from such.

However, he missed the point that both strategies occur each winter in a DWA because snow conditions influence the relative availability and value of forage, and mobility and forage consumption levels of deer change accordingly. It is because deer are energy-limited in DWAs that they should be expected to both maximize energy intake when possible and minimize energy expenditure when necessary to reduce energy loss and enhance survival; related behaviors will be dictated by snow conditions that influence mobility and forage availability. This is analogous to when a DWA "opens" and deer realize mobility and increase consumption and exploitation of better forage in a larger area.

Fawns especially should be expected to maximize energy intake whenever possible, and minimize energy expenditure because of their inherent disadvantages of small size, less body fat, and higher metabolic rate than adults (see beyond); this is why forage intake is most critical to fawn survival. Evidence of such is that consumption rates of fawns are higher and more efficient than adults (Pekins 1995). Interestingly, fawns in captivity gain weight throughout winter (Thompson et al. 1973) because of unlimited, high quality food, and most wild fawns receiving supplemental food maintained body weight for 20 days in northern NH (Tarr and Pekins 1998); activity of both was basically associated with foraging alone and provides an example of simultaneously maximizing energy intake and minimizing energy expense to achieve energy balance. Conversely, captive adult deer lose weight (body fat) in winter despite unlimited high quality food, further evidence of the physiological disadvantage of fawns. Presumably deer have circadian rhythms of the neuroendocrine system that promote seasonal body condition and fat cycles (Worden and Pekins 1995).

Much emphasis and concern was raised about the cost of locomotion in snow after the work of Parker et al. (1984) with trained elk and mule deer. Although their results clearly show the elevated energy costs of locomotion in deep snow, the more pertinent questions are: 1) how often do deer actually move through deep snow, and 2) what proportion of the daily energy expenditure of deer is spent on locomotion? Occupation of DWAs, and the creation of well-packed trails within, essentially minimizes high locomotion costs associated with deep snow. Access to food outside the DWA is limited by snow depths that preclude mobility, and deer isolated in a DWA do not move to better forage resources when mobility is restricted. Conversely, when snow conditions allow mobility, deer increase travel and activity to access food outside DWAs (Drolet 1976, Tierson et al. 1985, Nelson 1995). Therefore, relative to energy balance and survival, of most concern is the relative amount and cost of daily activity, not specific locomotion costs in deep snow.

Deer activity in winter can be considered foraging activity for all practical purposes (Beier and McCullough 1990, Bock 1993, Pekins 1995). Foraging activity has been measured by observing free-ranging wild, marked, released, and captive deer and typically averages 33-45% of daily activity (Beier and McCullough 1990, Bock 1993, Pekins 1995, Eckert 2004), but may be lower or higher depending on daily weather extremes; the remainder, and most importantly, the majority of time is spent bedded. Most activity is concentrated diurnally and in warmer times of the day (Ozoga and Verme 1970, Bock 1993, Eckert 2004), indirect evidence of an energy minimizing strategy as exposure increases thermoregulatory costs (Moen 1976). The energy cost of activity can be estimated by assuming that foraging is a combination of walking and standing, typically 15-25% above the cost of bedding (Fancy and White 1985). Mautz and Fair (1980) measured the energy expenditure of deer that spent >50% of a time period walking and their estimates were about 15% higher than the cost of bedding.

The estimated cost of activity for ungulates weighing 50-100 kg traveling <5 km/d is 17-23% of the FMR (Fancy and White 1985). These estimates suggest that the daily cost of foraging should probably not exceed the combined energy cost of all other daily energy costs (i.e., bedding, thermoregulation, digestion). However, estimating the daily energy expenditure of deer from activity budgets and associated costs invariably indicate that the cost of activity exceeds that of bedding, but typically are within 10% of each other (Bock 1993, Pekins 1995, Eckert 2004). This discrepancy may relate to assumptions and estimates made in measurements of both activity costs and energy budgets.

For deer in a DWA the basic assumption is that the elevated energy costs of moving through deep snow are minimized by the physical attributes of an optimal DWA. However, what is most important is that the daily cost of foraging, although not irrelevant, is basically stable (assuming good mobility and limited travel) because a 10% increase in foraging cost would require either a 50% increase in activity (Mautz and Fair 1980) or travel (Fancy and White 1985). Clearly this points to the advantage of higher activity and movement when possible to gain access to and increase consumption of forage. Because activity in winter is almost entirely associated with foraging and the associated energy costs of foraging are substantial in the daily energy budget, the abundance and distribution of canopy cover and forage that enhance mobility and optimize foraging activity within a DWA will simultaneously promote energy conservation and survival.

Seasonal Fat Cycles

The primary physiological adaptation of deer in response to dramatic seasonal changes in forage and environmental conditions is their annual fat cycle (Mautz 1978, DelGuidice et al. 1990b, Worden and Pekins 1995). This cycle is considered obligatory and controlled through the endocrine system by seasonal change in photoperiod; this adaptation is so strong that even fawns on restricted intake store appreciable fat (Verme and Ozoga 1982b, Abbott et al. 1984). Fat reserves are critical to winter survival and can be 20-30% of body mass of adult does in fall-early winter (McCullough and Ullrey 1983, Worden and Pekins 1995). Interestingly, body fat is <10% during summer, even in captive, non-lactating does fed *ad libitum* (Worden and Pekins 1995). Lesage et al. (2001) compared high and low density deer populations in Quebec and found contradictory results; larger deer were in the low density population, yet smaller fawns in the high density population had longer limbs and more body fat; these results seemingly indicate density-dependent influence and phenotypic advantage, respectively. However, because fawns in both populations had low body fat, high density fawns probably had no survival advantage.

The daily winter energy budget is the sum of DEI/MEI and the endogenous energy derived from catabolism of fat and protein tissue (Torbit et al. 1985); catabolism infers a negative energy balance due to loss of body mass. DelGuidice and Seal (1988) described three phases of undernutrition or negative energy balance; early, prolonged-reversible, and prolonged-irreversible. Although deer catabolize both fat and protein tissue during these phases, it is best described as a protein-sparing process where fat is nearly depleted prior to rapid protein and weight loss (Torbit et al. 1985, Del Guidice et al. 1987a, b, 1990b). Protein is actually conserved by urea recycling during winter because deer cannot meet their daily protein requirements from winter browse (Robbins et al. 1974b, Del Guidice 1987a, b, 1990b). Deer experiencing near complete fat loss begin to catabolize protein at a rapid rate that cannot be sustained long without nutritional recovery (Hershberger and Cushwa 1984, Torbit et al. 1985). For fawns, the relative contribution of body protein and fat to total endogenous energy is about 20-25% and 75-80%, respectively (Abbott et al. 1984, Torbit et al. 1985). Mautz (1978) suggested that fat may contribute 30% of the energy requirement of deer in winter.

Northern deer deposit fat (lipogenesis) during fall and subsequently catabolize fat (lipolysis) in winter to counteract their negative energy balance and weight loss due to restricted MEI. Even captive deer fed *ad libitum* realize this annual cycle. The highest MEI and rate of fat deposition (near doubling) of captive adult does occurs in September-October; in January-March their MEI was lowest and about 50% of the maximum in September-October, 43% of their body fat was catabolized, and they lost 15% body weight (Worden and Pekins 1995). Conversely, fawns in captivity grow continuously if provided optimal diets (Thompson et al. 1973); however, wild fawns consuming typical winter browse diets face an energy deficit like adult deer and are the first to succumb to malnutrition.

Fawns have less body fat than adults, both absolute and proportionally (Robbins et al. 1974, Verme and Ozoga 1980). Captive fawns fed natural browse diets for 4-5 weeks averaged 9% body fat in February (Tarr and Pekins 2002), and captive fawns weighing about 35 kg had about 10% body fat (Robbins et al. 1974). Body fat of wild fawns visiting supplemental feeding sites averaged 12.1% (range = 3-17%) in January-February (Tarr and Pekins 2002); it is doubtful that body fat of fawns exceeds 15% in winter.

Adult does have 2-3x as much body fat as fawns (% and absolute). Thus, on a relative scale, fawns have higher FMR and less endogenous energy than adults when facing a negative energy balance in winter, a distinct physiological disadvantage when forage is limited.

Adult and fawn deer can withstand large weight loss during winter, up to 20-30% body weight, although weight loss exceeding 20% is considered extreme, particularly for fawns. Starvation studies indicate that some fawns and adults can recover from >20% weight loss after >20 days without food (Hershberger and Cushwa 1983). Most captive fawns on restricted diets recover from weight loss of 10-20% (Mautz et al. 1976, Gray and Servello 1995, Taillon et al. 2006). Recovery of deer experiencing high weight loss is dependent on improved nutritional intake that is associated with timing of spring green-up and movement out of DWAs, indicating the potential and strong influence of winter length on energy balance and survival.

Daily Energy Expenditure

Estimates of the daily energy expenditure (DEE) provide a means to link habitat and winter conditions to the energy balance and survival of wintering deer. The DEE has been estimated with 1) DE and ME requirements for maintenance (e.g., Ullrey et al. 1970), 2) predictive models based on seasonal variations in body condition and processes and activity (e.g., Moen 1978), 3) carrying capacity models using nutritional and physiological data of deer relative to available forage nutrition (e.g., Potvin and Huot 1983), 4) energy budgets constructed from forage consumption and tissue loss (Bock 1993, Eckert 2004), 5) time-activity budgets (Bock 1993, Eckert 2004), and 6) the doubly labeled water (DLW) method that estimates carbon dioxide production over many days (Pekins 1995, Tarr and Pekins 2002, Eckert 2004). Most models and budgets require that researchers use limited data sets (often with many assumptions) because of the general lack of, and difficulty of physiological research with captive deer.

Three controlled studies with captive deer provide what should be considered standard values to compare estimates of DEE of wild deer; the maintenance energy requirements of adult does measured by Ullrey et al. (1970), fawns measured by Holter et al. (1977), and the DEE of adult does measured with DLW by Eckert (2004). Maintenance requirements were 548.5 and 640.6 kJ/kg$^{0.75}$/d for adult does (Ullrey et al. 1970) and fawns (Holter et al. 1977), respectively. The DEE of 8 captive adult does measured with DLW was 575.6 kJ/kg$^{0.75}$/d, a value only 5% greater than the maintenance requirement (Eckert 2004).

Surprisingly, most of the energy budget models have produced reasonably consistent estimates (±20%) despite the assumptions and limited data used in most. Models generally overestimate DEE (10-25%) relative to measurements of DEE with DLW (Eckert 2004); DLW measurements are considered superior because they are valid to ±8% accuracy (Nagy 1987). Arguably the greatest value of models is associated with identifying the most influential factors on energy balance, not DEE estimates per se. Most have consistently identified that consumption and forage availability have most influence on survival (e.g., Potvin and Huot 1983, Bock 1993), as have all studies with DLW (Pekins 1995, Tarr and Pekins 2002, Eckert 2004). Further, all have identified that deer show remarkable energy conservation strategies because their DEE expressed as a ratio of FMR is low (1.6-1.8 x FMR) and similar to their maintenance requirement. Although the DEE of fawns and adults are similar when expressed as a ratio to FMR (about 1.7; Pekins 1995, Tarr and Pekins 2002, Eckert 2004) indicating energy conservation behavior and strategy by both, because the FMR of fawns is higher than that of adult deer, the DEE of fawns is also proportionally higher.

The DEE can be partitioned to estimate the relative contributions of forage and tissue energy, and to assess the effect of length of winter on energy balance and survival. The contribution of forage represents, at best, only 50-65% of the DEE of adult deer based on forage nutritional data and consumption rates of wild and free-ranging captive deer (Schmitz 1990, Bock 1993, Gray and Servello 1995, Pekins 1995); this is basically equivalent to the FMR meaning that tissue (fat) energy must provide the additional energy costs of life, most notably foraging activity. Worden and Pekins (1995) estimated that 55-70 kg deer with 20% body fat would deplete their fat reserves in 90-100 days at average browse consumption rates. It is not coincidental that Potvin and Huot (1983) used 90 days in their carrying capacity model, and that ME requirements and number of confinement days were the most influential factors in their model.

Conversely, the relative amount and value of body fat in fawns (assuming 11% body fat) is much lower and represents only about 10-25% of their DEE (Fig. 2; Pekins 1995, Tarr and Pekins 2002). Thus, to maintain energy balance and limit loss of tissue energy (weight loss), fawns are much more dependent on forage consumption than adults, and forage availability and length of winter are unquestionably linked to fawn survival. That winter mortality of fawns is earlier and greater than adult deer is without question, and it is absolutely predictable from an energy balance analysis. Considering all data and studies, it is evident that measurable winter mortality should be expected when winter conditions that restrict forage availability and confine deer movement exceeds 90-100 days. Further, mortality rates will probably not be linear as winter lengthens beyond this time period, however, adult does have most resistance to winter mortality (Nelson and Mech 1986).

Stability and recovery of northern deer populations are most dependent on fawn survival and production by adult does, and the geographic range of deer is likely dictated by the influence of snow depth on these processes (Lesage et al. 2001). However, fawns and adult does address their negative energy balance differently, and habitat resources and winter conditions have variable influences on their survival strategies. Relative to adult does, winter survival of fawns is more dependent on MEI because they have higher FMR, less body fat, higher DEE on a relative basis, and less contribution to DEE from tissue energy. Conversely, although MEI is important to adult does and slows tissue depletion, length of winter is probably of most importance because adult does are adapted to withstand about 100 days of winter, primarily because of their high body fat. Further, the onset of exponentially increasing energy costs associated with gestation occurs in late March-early April (Pekins et al. 1998). Considering these relationships, and the direct relationship between snow depth and forage availability, management strategies to enhance MEI in DWAs will have most influence on fawn survival and also slow tissue

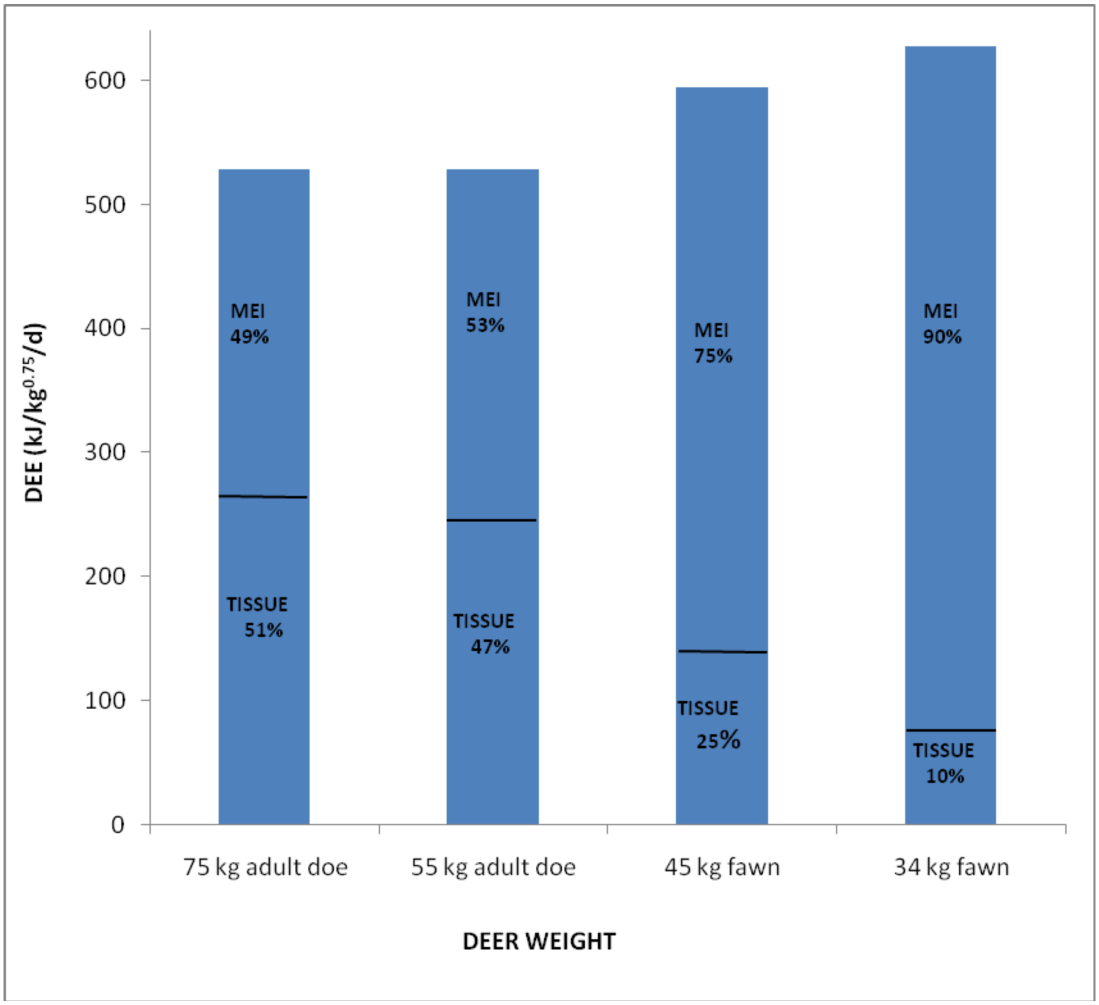

Figure 2. This figure depicts the winter daily energy expenditure (DEE) of free-ranging adult does and fawns as measured with doubly labeled water. Does and fawns partition their energy costs differently because fawns have higher DEE and less body fat. Forage intake is more important to fawns than adult does to minimize weight loss and promote winter survival. Because adult does are adapted to withstand more weight loss, length of winter has most impact on their condition, survival, and productivity. Data are from Pekins (1995) and Tarr and Pekins (2002).

depletion in adult does to promote productivity after lengthy winters. These conclusions from a bioenergetics perspective are in agreement with field studies conducted in New Brunswick (Morrison et al. 2002, 2003, Sabine et al. 2002), Quebec (Potvin and Huot 1983, Dumont et al. 2000, St-Louis et al. 2000), Michigan (Van Deelan et al. 1997), Minnesota (DelGuidice et al. 2002), and Maine (Lavigne 1999).

Predation

Principal winter predators of deer include wolves (*Canis lupus*), coyotes (*Canis latrans*), and bobcats (*Lynx rufus*) across the range of spruce-fir DWA. Occasional predation by lynx (*Lynx canadensis*) occurs but is considered opportunistic and uncommon (Quinn and Parker 1987, Fuller 2004). Bobcat predation is also considered opportunistic but more common than lynx predation, and is mostly by adult male bobcats (Litvaitis et al. 1984). Conversely, predation by wolves and coyotes is common, expected, and often has direct short and long-term influence on deer populations. Coyotes, bobcats, lynx, and black bears (*Ursus americanus*) all predate neonate deer, but such predation is usually considered opportunistic.

Predation is often linked to the evolutionary strategy of deer to occupy DWA (Nelson and Mech 1991, Kittle et al. 2008), and the influences of predation on winter survival of deer are complicated by the varied situations of the presence, density, removal, reoccupation, and appearance of predators in states and provinces. Long-term studies of wolf predation in Minnesota provide the foundation of understanding the principal, historical predator-prey relationship that wintering deer experience (see Nelson and Mech 1981). Range expansion by wolves within Minnesota and into Michigan and Wisconsin has focused recent research on the role of wolf predation on inexperienced deer populations (e.g., Van Deelen et al. 1997, DelGuidice et al. 2002). Likewise, recent appearance and expansion of coyote populations in the past 50 years throughout the range of spruce-fir DWA has focused much research on this "new" predator-prey relationship (e.g., Messier et al. 1986, Lavigne 1992, Patterson and Messier 2000). Multiple incidents of single wolves killed recently in New England have raised interest and concern about expansion and recovery of a regional wolf population, particularly about its potential effect on ungulate and predator populations.

The following brief description and interpretation of wolf predation on deer, and a more thorough description of coyote predation on deer, are not dissimilar. A recent analysis by Kittle et al. (2008) indicated that winter resource selection by deer is unlikely to be related directly to predation-risk, rather, their habitat use (i.e., occupation of DWA) reflects limited choice (or restriction) in forage and mobility. In fact, their use of winter habitat probably increases their predation risk, although that is debatable (Messier and Barrette 1985). In either case, the physical characteristics and resources within a DWA are related to relative risk, and pose the best defense against the potential limiting influence of winter predation on a deer population.

<u>Winter Predation by Wolves</u>

The impact of wolf predation on deer is of concern wherever wolves and deer coexist. The history of related research is >50 years old and even occurred in Wisconsin in 1950 after which wolves were extirpated (Thompson 1952)! Although debate exists as to the definitive, regulatory effect of wolf predation on deer, most studies conclude that hunter harvest and mortality from malnutrition in winter are the primary factors regulating deer populations (e.g., DelGiudice et al. 2006). However, there is little doubt that wolf predation of wintering deer affects size and dynamics of local and regional populations (Fuller 1990, see summary in Mech and Peterson 2003, DelGiudice et al. 2006). Essentially, a regional deer population reflects the combined and often interactive influences of natural and human-induced factors. Of interest is the fact that wolves have appeared singularly in New England states in the past decade, and breeding wolf populations in Canada are not geographically distant, but dispersal is inhibited by both geographic and human-related factors.

Wolves can perform "surplus killing" of deer in deep snow (DelGiudice 1998), but typically predate fawns and older deer that are either smaller, weaker, inexperienced, or in poorest condition (see summary in Mech and Peterson 2003, Mech 2006). Predation is directly related to winter severity, particularly as snow depth increases and mobility and condition of deer decline (Nelson and Mech 1986a, b). Essentially the risk of predation increases as winter lengthens and snow depth increases (DelGiudice et al. 2002). Importantly, predation in low density deer populations probably has more impact than in high density deer populations (Messier 1991). Deer management goals in areas of recovering deer and/or wolf populations need to reflect the relationships between and among winter severity, predation, winter habitat, and hunter harvest (DelGiudice et al. 2002).

Winter Predation by Coyotes

Coyotes are the principal predator of deer in New England and northeastern Canada, and are largely considered to have replaced wolves in the historical predator-prey relationship where wolves are extirpated across the range of spruce-fir DWA (Ballard et al. 1999). Coyotes kill deer within and outside DWA irrespective of winter conditions, and it is telling that much research of coyote predation had occurred in mild-moderate winters and predation rates are measurable. State and provincial deer declines have been linked to coyote predation in Maine (Lavigne 1992), Nova Scotia (Patterson 1994), New Brunswick (Parker 1995), and Quebec (Crete and Lemieux 1996).

Food habits of coyotes are much more diverse in mixed forest-agricultural habitat than contiguous forest. Given continuous snow cover, food choice in contiguous northern forests is extremely limited; long-term studies in NY indicate that coyotes shifted to a nearly complete deer diet over 20-30 years (see summary in Pekins 1992). A diet of deer is also nutritionally superior and should be preferred over snowshoe hare (*Lepus americanus*; Pekins and Mautz 1990, Pekins 1992). Coyotes predate deer largely because they have little choice; they are ill equipped to predate snowshoe hares in deep snow, the only alternative prey with measurable availability in northern forests during winter.

Essentially, both coyotes and deer face similar choices and problems at the northern extent of deer range; dramatic reduction in food diversity and availability, and limited mobility that influences access to food. Both deer and coyotes counteract these problems by occupying DWAs that provide better mobility, and most importantly, access to food. Thus, it is not surprising that coyotes have adapted to occupy DWAs, predate deer efficiently, and have measurable impact on deer populations.

The extent and impact of coyote predation is influenced by multiple factors including 1) sociality of coyotes (Messier and Barrette 1982, Messier et al. 1986, Parker and Maxwell 1989, Harrison 1992, Patterson and Messier 2000), 2) snow conditions (Parker and Maxwell 1989, Lavigne 1992, Patterson 1994, Patterson and Messier 2000), 3) the distribution, abundance, and vulnerability of deer (Messier and Barrette 1985, Brundige 1993, Whitlaw et al. 1998, Patterson and Messier 2000), and 4) the availability and abundance of alternative prey species (Patterson et al. 1998, Patterson and Messier 2000). Although influential to a degree and predated more in early winter, the availability and abundance of snowshoe hare seems to have little influence on coyote predation of deer (Patterson et al. 1998). Winter severity and snow conditions that restrict mobility of deer and the relative distribution, abundance, and vulnerability of deer most influence coyote predation of deer in DWAs.

Although groups of coyotes initiate more attacks on deer (Parker and Maxwell 1989, Patterson and Messier 2000) and appear to be more successful in killing deer (Messier and Barrette 1982, Messier et al. 1986, Parker and Maxwell 1989, Harrison 1992, Patterson and Messier 2000), there is minimal evidence that pair-bonding of reproductive coyotes is the primary cause of group formation or predatory success (Patterson and Messier 2000). Rather, it appears that coyotes have adapted to maintain groups or family units beyond fall, and these groups occupy DWAs prior to the reproductive season; also, single adult coyotes are more capable of killing deer than previously believed.

Clearly the vulnerability of deer to coyote predation increases with winter severity (Parker and Maxwell 1989, Lavigne 1992, Patterson and Messier 2000). Predation increases in extent and efficiency at end of winter as vulnerability of deer increases with deeper snow and their nutritional condition declines; not surprisingly, predation rates of deer are lower in winters with minimal snow. Coyotes kill deer of all sex-age classes and condition during winter (Messier et al. 1986, Lavigne 1992), and vulnerability is clearly highest for fawns because of their small size, inexperience, poorer body condition, and higher resource needs (Messier et al. 1986, Parker and Maxwell 1989, Ballard et al. 1999, Patterson and Messier 2003). It is important to note that adult deer in good condition can be highly vulnerable to predation, particularly in small DWAs (Potvin 1980, Lavigne 1992), in DWAs with low deer density, and in weather and snow conditions that hinder detection and restrict mobility and escape (Messier and Barrette 1985, Patterson and Messier 2000).

The fundamental question concerning the impact of coyote predation is whether it represents compensatory or additive mortality given that winter mortality is expected if deer occupy a DWA. Clearly the mortality rate of fawns is highest whether from malnutrition or coyote predation. Thus, predation is not necessarily additive if coyote predation is selective for deer predisposed to winter mortality. Supporting evidence and arguments for additive mortality are provided by Lavigne (1992), Whitlaw et al. (1998), Dumont et al. (2000), Patterson et al. (2002), and Patterson and Messier (2003). Further, strong evidence of declining regional populations in face of increasing coyote predation has been documented in Maine, New Brunswick, Nova Scotia, and Quebec (see above). However, because the relative vulnerability of deer is strongly related to winter conditions (i.e., snow and sinking depths), and variability in snow conditions within and among winters is common, coyote predation cannot be considered strictly additive every winter.

Assuming that additive mortality exists in certain winters, perhaps the more pertinent question is whether coyote predation has a long-term regulatory effect on deer populations. Conclusions from research in Quebec (Messier 1991, Dumont et al. 2000) and Nova Scotia (Patterson et al. 2002, Patterson and Messier 2003) were that coyote predation should be considered limiting not regulatory. Long-term regulation of deer population is believed to be density dependent and principally a function of competition for forage resources, presumably in DWAs unless summer-fall habitat is compromised (Dumont et al. 2000, Patterson et al. 2002, Patterson and Power 2002). Importantly this does not discount that coyote predation can be additive, rather, it indicates that it has a destabilizing effect on deer populations.

The history of deer and coyotes in southern Quebec provides evidence of both the limiting influence of coyote predation and the overall density-dependent regulation of deer populations. Coyote predation occurred as local deer populations grew in the 1970-80s, yet added to their subsequent regional decline (Crete and Lemieux 1996); however, current populations have recovered in face of continuous coyote predation (Dumont et al. 2000). The combination of consecutive mild winters, reduced density-dependent competition in DWAs, and local coyote control all contributed to the recovery of the regional deer population.

The annual influence of coyote predation will be depend mostly on winter severity and snow conditions, and perhaps as importantly, local deer density. Presumably the relative impact of coyote predation would be greater in low density populations, as in wolf-deer interactions (Potvin et al. 1988). A small, local or regional deer population, occupying small or suboptimal DWAs with limited forage resources and cover, would theoretically experience stronger limiting influence from coyote predation than a more robust population. Thus, coyote predation effectively lengthens the time of population recovery in depressed deer populations. The ability of that population to recover would likely be compromised until predation was effectively removed from that population, either naturally through a series of mild winters, or manipulatively through coyote reduction.

Within large DWAs, particularly in those areas with high deer density, an anti-predatory advantage exits due to the lower predator:prey ratio, and better mobility and detection that enables escape on complex trail systems (Messier and Barrette 1985). Predation rates of deer are higher in DWAs of low quality and small size (Potvin 1980, Lavigne 1992), in areas of low deer density within a larger DWA (Messier and Barrette 1985), and in areas of low deer density (Patterson et al. 1998, Patterson and Messier 2000). This inverse relationship between predation rates and deer density and abundance indicates that larger DWAs with moderate deer density should reduce vulnerability of deer.

Annual coyote predation should be ameliorated through effective management of DWAs because physical characteristics of DWAs influence predation. Essentially, coyote predation rates and the quality and condition of a DWA are inversely related. A DWA with optimal cover and forage resources should improve deer condition and mobility and indirectly temper the predation rate of deer, thereby reducing the potential additive mortality and limiting influence on the deer population. Thus, an optimal DWA with regard to minimizing coyote predation would be large, contain a reasonable density of deer (suggested as >2 deer/km^2, Patterson and Messier 2000), and provide adequate forage resources and cover that reduce malnutrition and promote mobility.

The majority of research and evidence supports the assumption that coyotes have replaced wolves in the historic predator-prey relationship throughout much of the northern range of deer occupying spruce-fir DWA. Thus, coyote predation has reduced the deer carrying capacity of much of the northeastern United States and Canada that had predator-less deer populations for decades. To expect that deer populations within this range will not be reduced periodically by high coyote predation that is directly related to winter severity seems unreasonable, as do long-term deer population goals that fail to account for coyote predation overall. Further, because neither deer nor coyotes were resident in northern Maine historically (Banasiak 1961), and both are a product of forest and land use change, there's legitimate debate as to the relative roles and importance of deer and moose in northern Maine. Regardless, the recovery of a depressed northern deer population requires conditions that allow the inherent high reproductive capacity of deer to act, essentially, a series of mild winters that simultaneously reduces competition for and increases availability of forage, and limits coyote predation.

Many attempt to explain winter survival of deer in terms of either density-dependence (forage competition) or density-independence (snow conditions, predation). Two studies provide insight into this question by investigating the interrelationships of deer population dynamics, forge competition, winter severity, predation, and hunting harvest at the northern extent of deer range in Quebec (Dumont et al. 2000, Lamoureux et al. 2001). After rapid decline in deer numbers in the early 1990s from a series of severe winters and high coyote predation, hunting was abolished and coyote control, habitat management, and winter feeding were initiated at two DWAs. The population dynamics of radio-collared deer were studied to assess whether density dependent (forage competition) or density-independent factors (snow conditions, predation) were most related to mortality, as well as the effects of reopening deer hunting. Forage competition was the most influential factor in one DWA where the population growth rate of deer was negligible; a clear conclusion was not possible in the other DWA with high population growth rate. Mortality of fawns was highest in both areas (starvation and predation), and surprisingly mortality of adult deer was not sex-specific, a surprising result given bucks-only hunting and condemning of hunter behavior.

Although these studies found that a density dependent response occurred in one DWA, clearly density-independent factors were also operating because snow depth largely dictates whether such responses (i.e., forage availability and competition) even occur in a DWA, and coyote predation occurred in mild-moderate winters. Because deer mobility and forage availability are functions of snow depth and winter severity, attempts to separate these factors seem illogical and pointless. Clearly, at the northern extent of deer range, both density-dependent and -independent mortality factors will have most effect on deer populations because their individual and combined impacts are more severe. Ironically, predation arguably reduces forage competition within a winter, and may actually reduce it long-term. Similarly, a built-in mechanism for long-term health and recovery of forage resources in a DWA may be severe winters that reduce access to forage, increase mortality, and reduce deer density in subsequent years (Potvin and Huot 1983). However, without question, DWAs that provide optimal size, cover, and forage resources will promote winter survival of deer while counteracting the regulatory and limiting influences of forage competition and predation.

Winter Severity Index (WSI)

Most states and provinces measure environmental parameters that are related to deer survival in DWAs to calculate a relative and temporal estimate of winter severity (winter severity index; WSI). The relationships between the WSI and winter mortality and herd productivity are used to predict the effect of winter weather on deer populations. Predicting these effects are essential for management purposes, particularly in setting subsequent harvest goals and strategies. The WSI should be directly related to winter mortality, and is often correlated with body condition (femur fat), fetal growth, and natality that are related to herd productivity (Verme 1977, Lavigne 1991, 1992a).

The relative value of a DWA can be evaluated by comparing WSI measurements within, among, and outside DWAs, as well as temporally as a DWA ages. The relative accuracy of a WSI probably varies relative to DWA age because forage and cover resources change temporally as a DWA ages (Chilelli 1988, MDIFW 2007). The most common measurements in a WSI are ambient temperature, snow depth, and sinking depth. Dumont et al. (2000) found that sinking depth summed over the winter was correlated with winter mortality in Quebec, and sinking depth and temperature may be adequate parameters to predict winter severity (MDIFW 2007).

Many states and provinces (e.g., MINN, NH, VT, WISC, ONT) simply sum the number of days with snow depth >15-18 inches and the number of days with ambient temperature <0° F; a total score of <50 equals mild, 50-79 equals moderate, 80-100 equals severe, and scores >100 equal very severe winters. Analysis of such scores provides a reasonable assessment of recent and long-term winter weather. The relationship between WSI and actual winter mortality is jurisdiction-specific, if not DWA-specific, because deer density is influenced by regional population goals, and the relative quality of a DWA varies as physical characteristics change with stand age. Of most consequence is the accuracy of the relationship between the WSI and winter mortality and production of deer in that jurisdiction/DWA.

The strong and direct relationships between and among snow depth, winter mortality, WSI, and occupation of DWAs indicate the usefulness and validity in using snow depth and/or WSI to identify regions and specific DWAs critically important to deer. Nelson (1995) argued for recognizing a critical snow depth that was related to time, in essence, linking WSI and winter habitat. In New Brunswick, deer range has basically been divided into two regions based on relative winter severity related directly to snow depth (40-50 cm threshold); DWA management is focused on canopy cover in the "severe" region and less so in the "moderate" region where mixed woods stands are believed to provide sufficient resources to wintering deer (Sabine et al. 2001). In Maine, the WSI was related to the winter mortality rate (WMR) in order to calculate a numerical impact on the population; after considering threshold WSI values (long-term WSI) and long-term WMR, regional harvest quotas are set to meet long-term population goals (MDIFW 2007).

The use of WSI in DWA management strategies seems advantageous from a number of biological and economic perspectives: 1) it is a numerical estimate that is strongly related to winter mortality of deer, 2) it indicates quantitatively the current and temporal biological value of regional and specific DWAs, 3) it provides a quantitative basis to compare the biological and economic value of a forest stand or DWA, 4) use of regional snow depth data may provide an easy and reliable method to identify regional needs and criteria for provision and management of DWAs, and 5) annual measurements of WSI provide for assessment and adjustment of its uses and applications. Many states and provinces already provide current WSI data and maps on-line to educate stakeholders about winter severity and deer mortality; identifying the role of DWAs in this relationship seems logical and worthwhile.

CHAPTER II: GENERAL BENEFITS OF DEER WINTERING AREAS

Deer residing within the spruce-fir region of the U.S. and Canada are truly at the northern limit of their geographic range. Where the ranges of deer and spruce-fir overlap, biologists identify winter weather as a main limiting factor that determines the size of regional deer populations, and ultimately, if deer will even persist (Verme 1973, Strong 1977, Boer 1978, Reay et al. 1990, Lavigne 1999, Wisconsin DNR 2001). Here, deer survival in winter is inextricably linked to the availability of habitats called "wintering areas" (DWAs) which allow deer to maximize their daily food intake, while minimizing the amount of energy they must expend to move, keep warm, and avoid predators.

While the specific composition of DWAs varies across the range, all are comprised by two basic habitat components: mature conifer stands which provide deer cover and improve their mobility, and other forest or non-forest habitats that provide deer with forage (Reay et al. 1990, Maine 1993, OMNR 2000b, NBDNR 2000) or opportunities to benefit from solar radiation (Aldous 1941, Severinghaus 1953, Beier and McCullough 1990). There are a number of basic, but important energetic benefits that deer get from the habitats they use as DWA.

Mature conifers represent the most important component of a DWA to deer wherever winter conditions are severe (Verme 1965, Reay et al. 1990, Lavigne 1999, OMNR 2000b, NBDNR 2002). The main reason is because dense conifer stands, especially those with a crown closure of at least 50%, provide deer with superior cover (Richens and Lavigne 1978, Alexander and Garland 1985) and improved mobility (Mattfeld 1974, Potvin and Huot 1983, Parker et al. 1984) as compared to deciduous stands, or mixedwood stands with lower conifer crown closure. Dense conifer stands are superior to others because they are especially effective at intercepting falling snow within their upper branches (Ozoga 1968, Lavigne 1999, Lishawa et al. 2007). This results in reduced wind speeds (Ozoga 1968, Reay et al. 1990), reduced radiant heat loss (Moen 1976), and higher mean temperatures than in more open stands (Ozoga 1968, Lishawa et al. 2007). Further, by intercepting falling snow, snow depths within conifer stands are often reduced (Potvin 1980, Nelson and Mech 1981, Reay et al. 1990, Lishawa et al. 2007), and can be as much as one third (Alexander and Garland 1985) to one half that in adjacent habitats with less conifer cover (Richens and Lavigne 1978). Snow that does eventually fall from the conifer branches is often partly melted and it tends to refreeze and compact when it hits the ground (Telfer 1978). This results in firmer snow that reduces the sinking depth of deer (Ozoga 1968, Lavigne 1999, Lishawa et al. 2007), and improves access to forage (Wetzel et al. 1975). Combined, these benefits mean that dense conifer stands allow deer to reduce their exposure and energy costs associated with foraging (Moen 1968, 1976, Tilghman 1989).

Throughout the spruce-fir range deer are regularly attracted to dense conifer stands during winter and they are frequently reported to congregate or “yard” within these stands, sometimes in large numbers (e.g., over 200 deer in one Michigan DWA, Ozoga 1972; >350 deer/km^2 in Maine, Lavigne 1999). Average deer densities in wintering areas in Ontario, New Brunswick, and Maine range from 6-61 deer/km^2 (see summary in Broadfoot et al. 1996). Yarded deer are able to establish and maintain a network of trails that may improve access to forage and reduce the energetic costs of foraging (Mattfeld 1974, Euler and Thurston 1980, Potvin and Huot 1983, Parker et al. 1984, Lavigne 1999). This is especially important for fawns because they have less access to browse than adult deer and their risk of death increases with snow depth (Nelson and Mech 1986, Fuller 1990, DelGiudice et al. 2002).

Complex trail networks in DWAs improve evasion from wolf and coyote predation (e.g., Nelson and Mech 1981, Messier and Barrette 1985). In Minnesota, wolf predation on deer is directly related to snow depth and is greatest in snow >60 cm (Nelson and Mech 1986, Fuller 1991, DelGiudice et al. 2002); well packed trails in DWAs enhance mobility and minimize activity in deep snow. Conversely, DWAs may actually increase the risk of predation to deer because predators are attracted to the abundance of prey within a concentrated area (Ozoga 1972, Dumont et al. 2000). While true, coyote:deer ratios are presumably lower in large DWAs which may effectively reduce the risk of predation to individual deer (Messier and Barrette 1985). Whitlaw et al. (1998) found no difference in predator-caused mortality between deer within and outside DWAs and concluded that the principal value of DWAs was to provide shelter and relative mobility to deer.

As a general rule, deer select wintering areas in landscapes that offer a variety of habitat options. In addition to using dense conifers for cover, deer take advantage of a variety of other microhabitats within a DWA that provide them adequate forage, and help them conserve energy under the wide range of environmental conditions they are exposed to during winter. Most conifer stands that serve as DWAs occur at low elevations, often below 600 m (Wetzel et al. 1975, Telfer 1978, Van Deelen et al. 1996, Lock 1997, NBDNR 2000, D'Eon 2001, Hurst and Porter 2008,), with many occurring along streams, rivers, or other water bodies (Gill 1956, Banasiak 1961, NBDNR 2002, W. Staats, personal communication). Not coincidentally, these locations provide optimal growing conditions for the tree species deer prefer as winter cover. For example, many DWAs in the Lakes States occur as low elevation "swamp conifer yards" which include cedar, balsam fir, white spruce, black spruce, and hemlock as their main components (Verme 1965, Wetzel et al. 1995, Van Deelen et al. 1996); all of these trees are well adapted to grow on wet sites. However, deer likely select cover at low elevations, in part, because higher elevation sites tend to have greater snow accumulation (Alexander and Garland 1985), and are colder, windier, and have longer winters (Weber et al. 1983).

While the majority of DWAs occur at low elevations, many are in areas with moderate-steep slopes. Specifically, deer often show preference for conifer stands growing on south-facing slopes (Gill 1956, Telfer 1978, Boer 1978, Potvin and Huot 1983, D' Eon 2001, MDIFW 1990, NBDNR 2000) where topography and conifer crown closure likely interact to protect deer from wind and convective heat loss (Severinghaus 1953, Euler and Thurston 1983, Voigt et al. 1997), and the southern exposure provides direct solar radiation (Alexander and Garland 1985, Reay et al. 1990). Most bedding sites in an Ontario DWA were located high up on both south-facing and north- facing slopes in areas where the best conifer cover was located (Armstrong et al. 1983b). Deer are known to forage in hardwood stands on steep slopes where wind has reduced snow depth and exposed fallen mast (e.g., acorns (*Quercus spp.)* and beechnuts (*Fagus* spp.) (Reay et al.

1990, Lavigne 1999, M. Tarr, personal observation) or browse (Schwab et al. 1987). Slopes may increase the vegetative diversity within a wintering area, thus providing deer with a variety of microhabitats they can use under a range of weather conditions Armstrong et al. (1983b). In some parts of the region (e.g., New Hampshire) deer may actively select wintering areas that include areas with slopes (Weber et al. 1983), while in others (e.g., Vermont), slopes may not be an important factor in deer wintering area selection (Alexander and Garland 1985).

In any DWA, deer are constantly selecting specific microhabitats that provide them the best energetic advantage for the current weather conditions and the current time of the day (Kucera 1976, Verme 1978, Armstrong et al. 1983b, Schmitz 1991). Deer conserve body fat in winter by timing their feeding activities for the warmest portions of the day and by decreasing their activity during cold weather (Beier and McCullough 1990, Schmitz 1991, Bock 1993). During the day, deer often forage in open hardwood stands which tend to have higher maximum day time temperatures as compared to dense conifer stands (Lishawa et al. 2007). During cold, but calm sunny days deer may move into open fields or other open habitats in an attempt to maximize their exposure to the sun, but they remain in dense conifer stands on days that are windy (Bier and McCullough 1990). Further, sites that deer use for bedding during the day are often in open areas exposed to the sun (Verme 1965, Armstrong et al. 1983a). At night, deer select bedding sites located close to conifer trees in dense conifer stands (Robinson 1960, Telfer 1967), often within the densest conifer cover available (Euler and Thurston 1980).

Biologists have long-recognized that habitat diversity within wintering areas is important for enabling deer to meet their energy requirements and to conserve body fat throughout winter (e.g., Gill 1956, Ozoga 1968, 1972, Verme 1973, Lock 1997, Sabine et al. 2001, Morrison et al. 2003). However, it is widely accepted that the extent to which deer use specific habitats within their wintering area, or if they choose to use a wintering area at all, often varies considerably from year to year and within any given winter in response to variations in winter severity (Beier and McCullough 1990, Pauley et al. 1993, Lavigne 1999, OMNR 2000b, Plante et al. 2004). Further, the type and proportion of habitats that deer use in areas where winter severity is generally mild-moderate, often differ from those used in areas where winter conditions are consistently severe (e.g., ONMR 2000, MDIFW 2007). This variability in winter habitat use has led to questions such as; what forest types provide the best cover for deer, how much conifer cover do deer actually require during winter, and what combination of habitats are optimal to ensure deer survive under a range of winter conditions (e.g., Potvin and Boots 2004)?

What conifer types provide best cover?

No study reports measurements to compare differences among conifer species to intercept falling snow or provide insulation from cold temperature and wind; most comparison is based on personal experience rather than formal measurement (e.g., Gill 1956, Telfer 1978). Cover value has been deduced by observing use or non-use during winter conditions when deer are expected to require cover (e.g., Weber et al. 1983, Lock 1997, Morrison et al. 2002, 2003). Most measurements of cover indices have been done to quantify the ability of conifer stands to provide cover relative to deciduous stands or non-forested habitats (e.g., Potvin and Huot 1983, Lishawa et al. 2007). What can be concluded from all of these studies is that a number of variables, including tree species, tree maturity, shape and height of tree crowns, % conifer crown closure, and stand size interact to determine the ability of any particular forest stand to provide winter cover for deer (Weber et al. 1983, Marston 1986, Reay et al. 1990).

The ability for any conifer species to provide cover is likely a function of the shape of its crown and stiffness of its branches and foliage that combine to determine whether it is most likely to hold or shed falling snow. In general, hemlock and northern white cedar are considered superior to other conifers in providing cover for deer (Gill 1956, Boer 1978, NHFSSWT 1997) due to their superior ability to intercept snow (OMNR 2000b). Balsam fir and spruce are moderate in their cover value, but may require denser stands to intercept the same amount of snow as hemlock and cedar (OMNR 2005, Gill 1956, OMNR 2000). Pines can provide suitable cover for deer, but often must grow in very dense stands to reduce snow depth (Voigt et al. 1997). Jack pine (*P. banksiana*) and red pine (*P. resinosa*) are poor cover (OMNR 2005), and tamarack and deciduous trees provide little to no cover for deer during winter (Gill 1956).

The relative proportion of softwood to deciduous trees in a stand influences its ability to function as winter cover for deer. In general, pure conifer stands provide better cover than stands with a lower proportion or no conifers (Richens and Lavigne 1978, Potvin and Huot 1983, Alexander and Garland 1985, OMNR 2000b). Further, mature conifer stands provide superior cover than younger conifer stands (Lock 1997, Morrison et al. 2002), and may have lower snow depths than deciduous stands of any age (Morrison et al. 2003). In Maine, mature conifers are considered those that are >35 years old (Lavigne 1999). Gill (1956) describes mature stands as those with trees that are either approaching or are of merchantable size. Numerous authors and management guides suggest that stands must be at least 10 m tall to provide functional cover (e.g., Boer 1978, Stadler 1987, Reay et al. 1990, Voigt et al. 1997). While the biological significance of this height is never explained, it does correspond to a height where trees within the stand are capable of having crowns large enough to intercept snow.

Throughout the spruce-fir region, deer predominately select mature forest stands dominated by conifers for cover, though the specific composition of those stands varies and usually reflects the dominant conifer species that occur within each region. For example, in northern New England, Quebec and Ontario including Anticosti Island, Nova Scotia and New Brunswick, the predominate conifer cover type is spruce-fir, and mature spruce-fir stands are regularly selected by deer for cover in these areas (NHFG 1970, Boer 1978, Alexander and Garland 1985, Lock 1997, NHFSWT 1997, Potvin and Boots 2004, Lavigne 1999, OMNR 2000b). For example, over 80% of deer yards in Maine are comprised of spruce-fir (Lavigne 1999). Eastern hemlock and northern white cedar comprise a smaller proportion of the forest cover in the spruce-fir region of these areas, and are often preferred for their cover value where available (Alexander and Garland 1985, Lock 1997, NHFSWT 1997, Lavigne 1999, OMNR 2000b, Lishawa et al. 2007). White cedar complexes and “swamp conifer yards” of cedar, hemlock, white spruce, and black spruce comprise the majority of the winter cover used by deer in Michigan and

Minnesota (Verme 1965, Ozoga 1968, Wetzel et al. 1975, Van Deelen et al. 1996, R. Horton, personal communication).

Mature stands provide superior cover over younger stands because they tend to be comprised of trees with large, fully developed crowns (Telfer 1978, Weber et al. 1983). Stands comprised of conifers with a large proportion of live crown, specifically those that have live branches abundant within 3-6 m of the ground, may provide deer the best insulation from heat loss and wind (Telfer 1978), though deer preference for such cover within this portion of the stand is not clear (Euler and Thurston 1980). Likely, the most important factor is the amount of live branches available to intercept snow in the upper portions of the stand as deer regularly select stands with a high proportion of conifer crown closure (Richens and Lavigne 1978, Alexander and Garland 1985, Lock 1994,). In general, conifer stands comprised of some combination of cedar, hemlock, balsam fir, or spruce provide the best cover for deer when the crown closure of those stands is at least 70% (Boer 1978, Euler and Thurston 1980, Marston 1982, Reay et al. 1990). Crown closure >60% may be adequate in hemlock and cedar stands due to their superior ability to intercept snow, while pine stands with >60% crown closure may have little effect on snow depth (Voigt et al. 1997). Euler and Thurston (1980) found that use of hemlock stands was maximum when crown closure was 71%, and suggested that the maximum ability of a stand to intercept snow occurs at crown closure of 60-70%.; stands with higher closure may not provide additional benefit. However, bedding sites are often located in very dense portions of conifer stands (Telfer 1967, Huot 1974, Armstrong et al. 1983b) where crown closure may reach 95% (Euler and Tester 1980), suggesting that dense stands near 100% crown closure may provide additional benefits to deer (Alexander and Garland 1985, OMNR 2005), such as reduced wind speed (Euler and Tester 1980) and radiant heat loss (Moen 1976).

While most authors and natural resource agencies seem to agree that conifer stands with at least 60-70% crown closure provide the best cover opportunities to deer there is a fair amount of debate in the literature regarding whether deer actually require this much cover. Numerous authors have suggested that solid conifer stands are not necessary for deer and are probably not optimal as a DWA (e.g., Weber et al. 1983, Alexander and Garland 1985, Lock 1997, Lavigne 1999, Potvin and Boots 2004,). In at least one area (Anticosti Island), deer density was shown to plateau or decline when conifer cover reached 50-70% (Potvin and Boots 2004). While providing cover for deer is a critical function of any DWA, adequate food must also be available for deer to best balance energy intake and conservation with energy expenditure (Ozoga 1968, Voigt et al. 1997). Deer likely select DWAs that allow them to optimize their use of specific habitats that provide cover and food under the range of weather conditions they are exposed to during typical winters. Pure conifer stands with dense crown closure may provide deer the best conditions for cover, but foraging opportunities are typically greater in stands that have less conifer cover with higher production of browse (Weber et al. 1983). In regions where winter conditions are typically severe, deer probably require a greater proportion of dense conifer stands than deer in areas where winter conditions are milder (Lavigne 1999, NBDNR 2002). Conversely, where winter conditions are milder, mixed conifer-hardwood (mixedwood) stands having considerably <60-70% crown closure may be more ideal (Gill 1956, MDIFW 1990, Morrison et al. 2002, Visscher et al. 2006).

Importance of snow depth

While a number of variables including snow depth, sinking depth, temperature, and wind speed combine to determine winter severity (Verme 1968, Lavigne 1999), reduced snow depth is consistently identified as the most important factor of functional DWA (Rongstad and Tester 1969, Telfer 1978, Pauley et al. 1993, Buss et al. 1997, Lock 1997, D'Eon 2001, Sabine et al. 2001). Deep snow influences deer activity primarily by reducing deer mobility (Gill 1956, Rongstad and Tester 1969, Buss et al. 1997, NBDNR 2005) and covering preferred forage (Potvin and Huot 1983, Beier and McCullough 1990). As a result, when snow is deep, deer are often described as selecting habitats that provide cover over those that provide food (Ozoga 1968, Rongstad and Tester 1969, Pauley et al. 1993, Sabine et al. 2001, Morrison et al. 2003, NBDNR 2005). However, this description is misleading and simplistic because deer abandon and occupy forest habitats in response to forage availability that is directly related to snow depth. When snow is deep the energetic costs of foraging in open habitats can far exceed the energy deer receive from food (Potvin and Huot 1983). Under these conditions, dense conifer stands are where deer are best able to access what browse is available while minimizing their energy costs of foraging. Further, some authors have suggested that when foods such as lichens and litterfall are considered, food availability within dense conifer stands may be as high as that in more open habitats (Ditchkoff and Servello 1998). Deer clearly select habitats that provide them the best access to food; when snow is deep, dense conifer stands provide such conditions, and often sufficient food resources to ensure winter survival.

Snow depth - how deep is deep?

In northern regions, snow depth increases both the risk of malnutrition and predation, and is the most important factor that determines deer winter mortality (DelGiudice et al. 2002). Snow of any depth can reduce deer activity and keep them in DWAs (Beier and McCullough 1990, Nelson 1995, Sabine et al. 2002). Snow depth of 25 cm can bury herbaceous vegetation and cause deer to concentrate their feeding activity in habitats that provide taller browse; this dietary shift increases the importance of conifer cover because deer spend more time bedded and ruminating a lower quality diet (Beier and McCullough 1990). In New Brunswick, surveys of DWAs before snow depth reached 40 cm underestimated the number of deer using DWAs because this depth stimulates most deer to migrate to their DWA (Sabine et al. 2002). At snow depths of 46-50cm, deer in Ontario become restricted within the core area of their DWA (Bruss et al. 1997). At depths >50 cm, deer movement becomes highly restricted (Gill 1956) and habitat use shifts strongly toward stands that provide cover (Morrison et al. 2003). Deer mortality should be expected at snow depth >100 cm regardless of the quality of the DWA (Gill 1956).

As a general rule, when snow depth exceeds 40-50 cm, deer use is restricted to the densest conifer cover available in a DWA (Rongstad and Tester1969, Drolet 1976, Parker et al. 1984, Broadfoot et al. 1996, Buss et al. 1997, Sabine et al. 2001, Morrison et al. 2003). In these conditions the active portion of a DWA is at its smallest and habitat use can be used to identify the best cover available to deer (MDIFW 1993, Buss et al. 1997, D'Eon 2001, Sabine et al. 2002). In these conditions alternate food sources such as lichens and litterfall may be especially important (Ditchkoff 1994) because they are often most available in mature conifer stands (Hodgeman and Boyer 1985), and are available when other forages are inaccessible (Ditchkoff and Servello 1998).

When snow depths are <40cm, mobility is less restricted and deer will range over a wider portion of the DWA to access more and preferred browse (Ozoga 1968, Rongstad and Tester 1969, Laramie 1993, Buss et al. 1997, Whitlaw et al. 1998, D'Eon 2001, Sabine et al. 2001, 2002); individual deer may actually leave their DWA (Rongstad and Tester 1969, Bier and McCullough 1990, Lavigne 1993, Nelson 1995). The active portion of a DWA is largest under these snow conditions (Buss et al. 1997)

The amount of cover that deer require varies based on the average winter conditions that deer are exposed to (Alexander and Garland 1985, Pauley et al. 1993, Lock 1997, Voigt et al. 1997, NBDNR 2000, NSDNR 2004, MNDNR 1986). In areas where winter conditions are generally mild and snow depth infrequently restricts deer movement, mature conifer stands with as little as 30% crown closure may provide adequate cover when weather conditions become severe (NSDNR 2004, NBDNR 2000). In areas where snow depth regularly restricts movement, conifer stands with >50% crown closure are probably required to provide adequate habitat during regular, severe winter weather (NSDNR 2004, Lavigne 1999, NBDNR 2000). Under both scenarios, browse should be interspersed within conifer stands to enable deer to maximize their forage intake when movement is restricted to conifer cover (Gill 1956, Voigt et al. 1997, Morrison et al. 2003).

How large do conifer stands need to be?

A final but critical variable in determining how much cover deer require during winter is conifer stand size; specifically, how large does a conifer stand need to be to provide functional cover? This question remains largely unanswered and we are unaware of any quantitative comparisons of stand function (i.e., snow interception, insulation from wind or snow) in comparable conifer stands of different sizes. Deer are known to use conifer stands as small as 0.4 ha when crown closure approaches 100% (Alexander and Garland 1985), but it is unclear how specifically crown closure and stand size interact to provide cover. Deer may select conifer stands that have large cores and small perimeters as winter cover (Morrison et al. 2003), but it is unclear what the minimum perimeter-to-area ratio of a conifer stands must be for it to provide functional cover over a range of environmental conditions, or to provide deer suitable protection from predators.

A number of authors (e.g., Boer 1978, Voigt et al. 1983) and some agencies (e.g., NBDNR 2000) provide recommended minimum stand sizes for managing conifer stands as DWAs. These recommendations appear to be based on observations of habitat use during typical winters, rather than any specific measures of habitat function. Caution should be used when attempting to infer habitat requirements from management recommendations, especially those based on observed use by deer; deer will readily select the best habitats available to them, even when those habitats may be less than optimal (Euler and Thurston 1980). Further, historic management recommendations for minimum cover sizes may be based as much on concessions to facilitate commercial timber harvesting, as on providing optimal cover conditions for deer (e.g., Gill 1956). Stand size may be important if for no other reason than larger stands are likely to support a greater concentration of deer than smaller stands (Potvin et al. 1981, Weber et al. 1983). Minimal functional size will likely vary based on a number of factors, including deer density (Potvin et al. 1981, Broadfoot et al. 1996), predator abundance, tree species composition, stand height and crown closure, position on the landscape (including elevation, aspect, slope) which determines exposure, and average weather conditions of the area in which the stand occurs.

Size of DWAs

Across spruce-fir range DWAs range in size from small "pocket yards" <5 ha (Banasiak 1961), to large complexes >8000 ha (Lavigne 1999). The actual size of any DWA has been described as constantly "expanding and shrinking" as the degree to which deer are restricted to dense conifer stands changes in response to winter severity (Potvin et al. 1981). As a result, the portion of a DWA occupied by deer should be expected to differ annually, within any winter (Beier and McCullough 1990, Pauley et al. 1993, Lock 1997, D'Eon 2001, Morrison et al. 2003), and daily based on changes in weather and snow conditions; e.g., sinking depth and mobility can change hourly (Potvin and Hout 1983).

Foraging activity in deep snow

During periods of deep snow deer are restricted to dense conifer cover within a DWA and remain within or close to dense cover. Foraging activity will generally be concentrated on forage available immediately under or within close proximity to conifer cover (Reay et al. 1990, MDIFW 1993, Dumont et al. 2005), suggesting that deer may select conifer cover based on its proximity to suitable browse (Gill 1956, Euler and Thurston 1980, Van Deelen 1999, Morrison et al. 2003). When snow is deep, deer selectivity for browse is very low and they will forage on nearly any woody browse that is available (Brown and Doucet 1991, Potvin et al. 2003, Dumont et al. 2005, Tremblay et al. 2005, Tallion et al. 2006, Sauvé and Côté 2007). As a result, when deer density is high, or when deer are confined for long periods, food availability in dense conifer cover can become extremely limited (Banasiak 1964, Lock 1997), and perpetual over-browsing and compromised forage resources occur.

Importance of lichens and litterfall

When browse becomes limited, alternate food sources may become especially important for helping deer survive winter (Ditchkoff and Servello 1998). Throughout winter, but especially when deer are confined to dense conifers, arboreal lichens and litterfall may comprise a significant proportion of their diet (Ditchkoff 1994, Ditchkoff and Servello 1998, Potvin et al. 2003, Voigt et al. 1997, Tremblay et al. 2005, Ward and Marcum 2005). Arboreal lichens grow mainly on live tree branches, so lichen biomass tends to be greatest on tall trees that have a large proportion of live crown (Lang et al. 1980, Neitlich and McCune 1997). As a result, lichen biomass tends to be higher in mature stands than in young stands (Tremblay et al. 2005). Over-mature stands with numerous dead and dying trees may provide the best source of available lichens to deer, as large amounts of lichens fall on sloughing bark, and falling tree boles and dead branches (Lang et al. 1980). Further, many lichens grow on deciduous trees, so conifer stands that contain at least a few deciduous trees may provide more lichens than pure conifer stands (Neitlich and McCune 1997), though it is unclear if lichen species that grow on deciduous trees are consumed by deer. While the availability of lichens and litter may be unpredictable at any given time (Ditchkoff and Servello 1998), they offer deer a relatively stable, annual food source (Tremblay et al. 2005, Ward and Marcum 2005), and deer may occupy DWAs based on past consumption patterns (Ward and Marcum 2005).

Foraging activity at moderate-low snow depth

When snow depths are moderate, deer often use stands comprised of both conifers and deciduous trees (Reay et al. 1990, Morrison et al. 2002). Mixedwood stands generally provide more browse than conifer stands (Visscher et al. 2006) and they often contain some conifers large enough to provide cover (Morrison et al. 2002). Although mixedwood stands provide less cover than dense conifer stands and less browse than regenerating stands, they are often the only stands that provide both browse and cover simultaneously (Morrison et al. 2002)

When snow depths recede, or when hard crust allows deer to walk on top of snow, they become mobile and will range throughout a DWA to access more habitats and browse (Gill 1956, Banasiak 1961, Lavigne 1976, 1999, Morrison et al. 2003). When snow depth is not restrictive, browse availability is generally greatest in regenerating stands, moderate in mixedwood stands, and lowest in mature conifer stands (Monthy 1984, Morrison 2002, Visscher et al. 2006). Large clearcuts often provide a substantial amount of browse and deer take full advantage of this food when conditions allow (Wetzel et al. 1975, Lavigne 1999, Van Deelen 1999) Deer readily browse in partially harvested stands (Monthy 1984) and will use open deciduous stands where they feed on browse and fallen mast (Rongstad and Tester 1969, Wetzel. et al. 1975, Beier and McCullough 1990, Visscher et al. 2006).

Deer abandon DWA in spring when snow conditions provide improved mobility. Sinking depth in spring can be as influential as snow depth because snow density and compactness is affected by warmer spring temperatures; deer are generally dispersed at snow depths <30 cm (Nelson 1995). Deer typically migrate from a DWA in spring and return to their summer range within a week of bare ground appearing in open habitats (Verme 1973, Lewis and Rongstad 1998, Sabine et al. 2002) and when mean temperatures are consistently above freezing (Beier and McCullough 1990). Deer may forage in open habitats including bogs (Beier and McCullough 1990), agricultural fields (Rongstad and Tester 1969, MDIFW 1993, OMNR 2000b), and blueberry plains (Skinner and Telfer 1974) at low snow depth. These habitats are especially important in spring when deer are most likely to succumb to malnutrition (DePerno et al. 2000, Dumont et al. 2000, DelGiudice et al. 2002), and need high quality forage to recover body condition (Verme 1962). Hardwood stands and open fields are often the first habitats to lose snow in spring and to provide green vegetation when deer migrate from DWAs and return to summer range (Ozoga 1968, Schwab et al. 1987). Deer may return briefly to their wintering area during late winter storms (Tierson et al. 1985) or when temperatures fall below freezing, though return is not always associated with any obvious weather change (Beier and McCullough 1990).

Traditional use of DWAs

Throughout their range, individual deer show strong fidelity to the specific sites they use as a DWA (Rongstad and Tester 1969, Verme 1973, Lavigne 1991, NBDNR 2002, Morrison et al. 2003, Van Deelen et al. 2005). In at least one case, many generations of deer have returned to the same DWA for >100 years (Dickinson and Severinghaus 1969 cited in MDIFW 1990, Table 18). Reports of deer using the same DWA for 30+ years are common in many areas including New Brunswick (Whitlaw et al. 1998), Maine (Lavigne 1991), New Hampshire (W. Staats, personal communication), New York (Severinghaus 1953), Michigan (Verme 1973), Wisconsin (Kabat et al. 1953), and Minnesota (Rongstad and Tester 1969). However, not every DWA is used annually by deer (Gill 1956, C. Hulsey, personal communication).

Migration to DWAs

Long-distance migrations between summer range and DWAs are common. For example, deer migrate 32-40 km in New Hampshire (W. Staats, personal communication), 36 km in Ontario (Broadfoot et al. 1996), 31 km in Minnesota (Rongstad and Tester 1969), 37 km in Wisconsin (Hoskinson and Mech 1981), 22 km in New York (Hurst and Porter 2008), and 95 km in Quebec (Pichette and Sampson 1982 in MDIFW 1990, Table 19). The average distance that deer migrate between summer range and their DWA is frequently 10+ km (NHFG 1970, Verme 1973, MDNR 1986, Oyer and Porter 2004), but some deer don't migrate at all, but occupy the same range year-round (Beier and McCullough 1990).

Snow depth and minimum daily temperature have been suggested as the most important factors that stimulate deer to enter their DWA (Tierson et al. 1985, Nelson 1995, Buss et al. 1997, Voigt et al. 1997, Sabine et al. 2002). However, snow depth is likely the most important factor that ultimately determines if deer will migrate and remain in their DWA (Rongstad and Tester 1969, Sabine et al. 2002). Sabine et al. (2002) suggested that in areas where winter conditions are predictably severe, a combination of cues including snow depth, temperature, and photoperiod may combine to stimulate deer to migrate. However, snow accumulation in early-winter may be a strong enough stimulus alone to cause deer in these areas to migrate, because it serves as a cue to the approach of almost certain limiting weather conditions (Sabine et al. 2002). In parts of northern New Brunswick and Ontario where winter is consistently severe, deer begin migrating at snow depths as low as 10 (Sabine et al. 2002) and 20 cm (Buss et al. 1997, Voigt et al 1997), respectively.

In areas where winter conditions are typically mild to moderate, many deer delay migration until snow depth actually begins to limit mobility (Sabine et al. 2002). For example, in the Adirondacks and southern New Brunswick, deer may not migrate until snow depths are at least 38 cm (Tierson et al. 1985, Sabine et al. 2002). If winter conditions turn mild and snow recedes, some deer may vacate the DWA (Nelson 1995). During winters when conditions are variable, individual deer may migrate back and forth multiple times between their summer range and DWA in response to changing snow conditions (Rongstad and Tester 1969, Sabine et al. 2002). Further, it is not uncommon for some deer in these areas to remain on their summer range all year if winter conditions remain mild (Beier and McCullough 1990, Sabine et al. 2002). As a result, some DWAs aren't used every year, but are likely critical during deep snow conditions (Gill 1957).

Obligatory and conditional migration

The term conditional migration is used to describe those populations that do not migrate consistently, and this behavior has long been recognized (Cook and Hamilton 1942, Drolet 1976). Conditional migration occurs when a regional climate produces variable snow conditions not requiring consistent use and confinement in a traditional DWA (Sabine et al. 2002). Populations of deer in areas where yearly snow conditions are extremely variably are often comprised by a combination of "obligatory migrants" – deer that migrate to their wintering area in early winter and remain there until spring – and "conditional migrants" – deer that may or may not migrate, and may or may not remain in their wintering area when they do (Tierson et al. 1985, Nelson 1995, Nicholson et al. 1997, Van Deelen et al. 1998, Sabine et al. 2002). Conditional migration is rare for deer living in areas where weather conditions are predictably severe; most deer in these areas migrate to their wintering area in early-winter and remain there until spring (Nelson 1995, Sabine et al. 2002).

Deer that travel only a short distance between summer and winter range are more likely to be conditional migrants than deer that travel long distances (Sabine et al. 2002). Migration distance is likely related to the quality and variety of the habitats available to individual deer on their summer range; deer are less likely to migrate long distances if their summer range provides a good interspersion of forage and cover that allows them to meet their needs under a variety of weather conditions (Verme 1973, Tierson et al. 1985, Van Deelen 1999, Plante et al. 2004). In New Brunswick, non-migrants had home ranges that included dense hemlock and cedar stands which were absent on the summer ranges of deer that migrated to a separate wintering area (Sabine et al. 2002).

Survey methods of wintering deer need to account for abundance and location of conditional migrators that use non-traditional winter habitat, such as mixedwood stands in mild-moderate winters (Sabine et al. 2002). Ironically, identification of DWAs occupied in severe winters becomes more essential, yet problematic in such areas (Sabine et al. 2001). However, the infrequency of conditional migration or the obligate migration of most northern populations is indicative of the influence of snow on deer use and dependence on traditional DWAs.

Role of sex/age-class in migration

The question of continual use and fidelity of a DWA is an important concern because most DWAs have a finite usefulness either due to breakdown from aging or timber harvest. There seems to be general agreement that there is no significant difference in migration behavior between different sexes or age-classes of deer (Verme 1973, Tierson et al. 1985, Beier and McCullough 1990, Van Deelen et al. 1998, Hurst and Porter 2008). Although, mature bucks may remain on their breeding territory after most other deer have migrated, and are often among the last deer to enter the DWA (Verme 1973, M. Tarr, personal observation) Because of the social hierarchy of deer (Hirth 1977), female fawns follow their mother to a DWA and tend to return thereafter; buck fawns have less fidelity to their initial DWA because of their subsequent dispersal patterns as yearlings (Nelson and Mech 1981, 1984, Tierson et al. 1985, Nelson 1998). Conditional migration may be common in hunted populations because orphaned fawns may not learn traditional migration patterns (Nelson 1995, Aycrigg and Porter 1997).

Site fidelity and importance of kin groups

In general, once deer have learned the location of their DWA they often return to it for life (Aycrigg and Porter 1997) and may migrate through other suitable winter habitat (Tierson et al. 1985). This fidelity toward specific seasonal ranges is believed to be largely the result of the tight social bonds they form with other deer in "kin groups", which are groups of deer typically comprised by at least one dominant adult doe and anywhere from 2 to 14 of her relatives (Aycrigg and Porter 1997, Taillon and Côté 2007). By associating with a dominant doe, less experienced and subordinate deer may get access to resources that might otherwise be unavailable to them (Taillon and Côté 2007). Further, once in a kin group, deer quickly establish a dominance hierarchy which reduces conflicts between individual deer and minimizes the energetic cost of fighting (Ozoga

1972). Once established, an individual's place within that dominance hierarchy may be retained for life and this likely strengthens the bond between deer within each kin group (Taillon and Côté 2007). Tierson et al. (1985) suggested that the stable social structure provided by kin groups may be so important to deer that they establish their seasonal ranges based more on social factors than on habitat types.

Deer are often reluctant to abandon their established DWA for another suitable DWA (Gill 1957, Verme 1973, Voigt et al. 1997, Van Deelen et al. 1998). For example, when all deer within a kin group are removed from their range, deer density may remain low for as many as 5 years before deer from adjacent kin groups or offspring of the original females colonize the area (Oyer and Porter 2004). As a result, habitat improvements made on areas currently unused by deer are unlikely to result in rapid influx of deer (Beier and McCullough 1990) and may be less cost-effective than improvements made to occupied DWAs (Tierson et al. 1985). However, non-occupation of a traditional DWA does not reflect its future use and importance, but may simply indicate mild winter conditions precluding the necessity of use, low deer density, or behavioral choice. For example, in certain winters deer maintain mobility and/or move to exploit forage resources associated with timber harvests (Verme 1973, Drolet 1976, Tierson et al. 1985, Van Deelen et al. 1998).

Influence of deer social structure

Any local deer population is likely comprised by a number of deer kin groups, each with its own summer and winter ranges (Tierson et al. 1985, Sabine et al. 2001, Aycrigg and Porter 1997). In any DWA a number of kin groups will generally congregate in the same general area, but maintain discrete home ranges that may overlap with those of adjacent kin groups, especially when deer density within the DWA is high (Ozoga 1972, Tierson et al. 1985, Van Deelen et al. 1998, Sabine et al. 2001). In high deer density, deer from separate kin groups may encounter one another frequently, and a single social hierarchy likely develops within the DWA to reduce aggressive encounters (Ozoga 1972, M. Tarr, personal observation).

When deer disperse from their DWA in the spring they generally make straight-line movements back to the summer range occupied by their kin group (Rongstad and Tester 1969, Verme 1973, Van Deelen et al. 1998). However, deer from any DWA may travel in all directions when they disperse (Rongstad and Tester 1969). This means that groups of deer that yard together in the same DWA often occupy different summer ranges, which may overlap, or be widely separated (Aycrigg and Porter 1997). Throughout the spruce-fir region, size of DWAs averages only 5-15% the size of summer range (MDIFW 1993, Broadfoot et al. 1996, Voigt et al. 1997). As a result, in northern areas where some deer travel long distance between their summer and winter ranges, factors that affect the survival and productivity of deer within a local DWA may actually affect deer over a much larger geographic area (Verme 1973, Broadfoot et al. 1996, Voigt et al. 1997, Morrison et al. 2003). If those factors result in high winter mortality, deer density in areas far removed from the DWA may remain low for a considerable period of time (Verme 1973, Van Deelen et al. 1998, Oyer and Porter 2004).

Factors that affect use and quality of DWAs

Those DWAs that receive traditional use often retain desirable cover and foraging opportunities over a long period of time (Maine 1993). Size, natural forest succession, browsing, development, supplemental feeding, and timber harvesting may all influence the ability of a DWA to support deer long-term. The following are brief summaries of how these factors may contribute to the long-term viability of a DWA.

Importance of DWA size

In general, large DWAs tend to be used by deer for a longer period of time than small DWAs (Germaine et al. 1986). Deer are most likely to abandon DWA <100 ha because of increased risk of predation and malnutrition (Goodreault 1975, Mech and Nelson 1981, Messier and Barrette 1983, Boer 1992). Larger DWAs also tend to support larger numbers of deer (Potvin et al. 1981, Weber et al. 1983, Boer 1992, Broadfoot et al. 1996). More deer within a wintering area may reduce the predation risk to any individual deer (Messier and Barrette 1985) and reduce the individual energy costs of establishing and maintaining trails throughout the DWA (Mattfeld 1974).

Stand maturation

Conifer stands comprised of tall trees with full crowns that provide dense crown closure provide the best winter cover for deer. As conifer stands become over-mature, crown closure within these stands is reduced when individual trees die and fall. This reduction in crown closure reduces the cover value of over-mature stands by reducing their ability to intercept snow and insulate deer from wind and cold temperature (Verme 1965, Boer 1992). Deer should be expected to abandon stands where critical cover has been reduced below the minimum level needed to meet their requirements (Gill 1957, Boer 1992, Lavigne 1999). State and provincial deer biologists in Vermont, New York, and New Brunswick consider over-maturity a significant factor influencing the quality of DWAs in their respective regions (S. Haskell, personal communication; J. Hurst, personal communication; R. Cumberland, personal communication). Lack of active management was given as the main reason why DWAs became over-mature. Boer (1992) showed a 5% annual attrition rate in wintering areas in New Brunswick as the result of natural stand maturation. He concluded that DWAs where no timber harvesting occurred were more likely to be abandoned than those where timber harvesting was used to maintain the cover component within conifer stands. As stands become over-mature, their susceptibility to damage from insects and diseases increases, and this can result in additional loss of cover and further reduction in quality of the DWA (Lavigne 1999).

Insects and diseases

There are a few important insects and diseases of spruce-fir that can result in loss of important conifer cover in DWAs.

Spruce budworm

Spruce budworm (*Choristoneura fumiferana*) is a defoliator that attacks white spruce, red spruce, and balsam fir (Talerico 1984). Balsam fir is most susceptible and least resistant to injury followed in order by white spruce, red spruce, and black spruce (Whitter et al. 1984). This insect kills trees by repeatedly removing the current year's foliage and most trees will die when they have lost >75% of their total foliage (Whitter et al. 1984). In 1977-1988, spruce-fir forests throughout North America were affected by a spruce budworm outbreak (Irland et al. 1988) that reduced both the availability and quality of winter cover for deer (Alexander and Garland 1985, Boer 1992, Lock 1997, Lavigne 1999). In Quebec, spruce budworm defoliation resulted in the complete loss of overstory balsam fir and white spruce from some wintering areas (Boer 1992). Consequently, areas that once provided functional winter cover were converted to stands of young, intolerant hardwoods (Reay et al. 1990, Lock 1997, Lavigne 1999). Although this increases the amount of browse available to deer, it often results in a long-term loss of cover in these stands (Dumont et al. 2000). Certain large DWAs that were severely damaged by spruce budworm became fragmented into smaller "pocket yards" that were less effective in preventing malnutrition and predation (Potvin et al. 1981, Alexander and Garland 1985).

Many landowners and timber companies conducted extensive timber harvests to salvage damaged trees and limit additional losses; as a result, many of these stands were converted into marginal DWAs (Alexander and Garland 1985, Gadzik et al. 1998, Lavigne 1999). Extensive timber harvesting in budworm-damaged stands is related, in part, to loss of >50% of the DWAs in northern Maine (Lavigne 1999), and subsequent decline of the associated deer population (MDIFW 2007). It has also substantially reduced that capacity of the remaining DWAs to provide functional winter cover for deer (C. Hulsey, personal communication; L. Kantar, personal communication).

Spruce budworm outbreaks tend to oscillate in cycles (Talerico 1984) that mimic the typical lifespan of balsam fir (K. Lombard, personal communication.). Over-mature conifer stands containing a large proportion of trees in poor health are especially susceptible to budworm (Frank and Bjorkbom 1973, Boer 1992). Throughout the spruce-fir range, many over-mature conifer stands regenerated as even-aged stands following the 1977-1988 outbreak; thus, in the absence of any other disturbance (e.g., timber harvesting that increases the diversity of forest age-classes), large areas of spruce-fir will mature simultaneously creating the likely scenario for another large-scale spruce budworm outbreak (Irland et al. 1988, Gadzik et al. 1998, Lavigne 1999,).

Over-mature stands that contain a high component of balsam fir are most susceptible to spruce budworm damage (Whitter et al. 1984, K. Lombard, personal communication). In Maine, fir is considered pathologically mature as early as 50 years along the coast, and as early as 60 years in the interior and north (Frank and Bjorkbom 1973). Therefore, the most effective way to protect stands from budworm is to encourage vigorous, multi-aged stands comprised of a combination of spruce, fir, and non-host species (Whitter et al. 1984). Stand susceptibility can be reduced further by encouraging spruce and other conifers such as hemlock and cedar over balsam fir, whenever possible (Gill 1957, Frank and Bjorkbom 1973, Alexander and Garland 1985, Reay et al. 1990). Harvesting fir for pulpwood before it deteriorates is an effective way to reduce the proportion of fir in spruce-fir stands (Frank and Bjorkbom 1973). Vigor in young spruce-fir stands can be improved through early thinning and by removing competing hardwoods (Reay et al. 1990).

Balsam woolly adelgid

Balsam woolly adelgid (BWA, *Adelges piceae*) is an exotic sucking insect that has caused extensive damage to true firs (*Abies* spp.) throughout North America, but balsam fir is the only native fir that is susceptible to this insect in the northeast and Canadian provinces (Ragenovich and Mitchell 2006). Firs infected with BWA suffer from severe stem and twig injury that causes reduced growth, reduced cone and seed production, and loss of needles (Ragenovich and Mitchell 2006). While infected firs may survive for a decade or more (Ragenovich and Mitchell 2006), this insect causes nearly 100% mortality over time (K. Lombard, personal communication). In Maine, entire stands of overstory and understory fir have been killed from the coast to Aroostook, Penobscot, and Piscataquis counties in the north (DCMFS 2008a).

Temperatures <-3° C kill any BWA exposed above the snow (Ragenovich and Mitchell 2006); however, mild winters may allow this insect to reach damaging levels (DCMFS 2008a). In the northeast, fir stands below about 1000 m in elevation tend to be most susceptible to injury (K. Lombard, personal communication) which means that nearly all DWAs containing fir are vulnerable. However, healthy firs growing on primary fir sites (see Where do spruce-fir grow? in Chapter 3) are less vulnerable to injury than slow-growing trees on less suitable sites. Aside from encouraging conifers other than fir, there is little that can be done to protect forest stands from BWA (Reay et al. 1990, K. Lombard, personal communication). Infected stands should be harvested in the winter when BWA are unable to leave trees; trees should be cut and tops left on the ground so the insects die (K. Lombard, personal communication). If infected trees are cut in summer, BWA is capable of crawling from cut trees and infecting other trees in the stand (K. Lombard, personal communication).

Other pests

Other pests of spruce-fir include *Armillaria* root rot fungus (*Armillaria ostoyae*) (Reay et al. 1990), and diseases such as red ring rot (*Fomes pini*), red brown rot (*Polyporus schweinitzii*), and the fungus *Stereum sanguinalentum* that causes "red heart" disease (Frank and Bjorkbom 1973). All of these pests enter spruce-fir trees either through broken tops, broken branches, or damaged roots or tree stems (Frank and Bjorkbom 1973); these are all common symptoms in over-mature stands or those that have suffered damage from wind, snow/ice, or logging. As with spruce budworm and BWA, the best way to minimize pests is to maintain uneven-aged spruce-fir stands in a healthy vigorous condition through periodic timber harvesting (Frank and Bjorkbom 1973, Reay et al. 1990, K. Lombard, personal communication).

Deer browsing

Deer frequently congregate in DWAs at densities exceeding 20 deer/km^2 throughout spruce-fir range (see summary in Broadfoot et al. 1996). Browsing by deer confined at these densities for extended periods of time can often reduce the amount of food available to each deer and lead to increased malnutrition, especially in fawns (Banasiak 1964, Maine 1993). In an attempt to meet their energy needs, deer may browse trees and shrubs beyond the current annual growth, which can reduce the amount of browse available in future winters (Dumont at al. 2000, Dumont et al. 2005) and reduce the carrying capacity of the DWA.

Selective browsing that favors plant species that are either unpalatable to deer or are tolerant of browsing can alter the forest composition in DWAs (Van Deelen et al. 1996, Van Deelen 1999, Sage et al. 2003, Tremblay et al. 2005). For example, northern white cedar and hemlock are so highly preferred as browse that they are nearly impossible to regenerate (Aldous 1941, Gill 1957, Brown and Doucet 1991, Van Deelen et al. 1996, Voigt et al. 1997). Many white cedar stands that function as DWAs today were likely first established during a period when deer density was very low (Van Deelen et al. 1996).

Development and supplemental feeding

Road construction and commercial and residential development can reduce the total amount of habitat available to deer (MDIFW 1990, Reay et al. 1990, K. Gustafson, personal communication) and reduce the quality of the habitat that remains. This reduces the number of deer that can be supported and increases deer pressure on remaining undeveloped areas (Reay et al. 1990). Parcelization of habitat into smaller fragments makes it difficult to manage forested deer habitats economically through commercial timber harvesting. Further, the incidence of supplemental feeding increases where deer and people live in close association (M. Tarr, personal observation).

Supplemental feeding has been shown to disrupt the migration patterns of deer and may cause them to alter the specific area that they use during winter (Lewis and Rongstad 1998, Tarr and Pekins 2002, Hurst and Porter 2008). In Minnesota, about 25% of deer remain on their summer range and this may be due in part to supplemental feeding (Rick Horton, personal communication). In Wisconsin, deer provided supplemental food on their summer range migrated to their DWA as many as 19 days later than non-fed deer, though deer with access to supplemental food in winter did not delay their spring migration back to their summer range (Lewis and Rongstad 1993).

Deer in the Adirondacks were shown to shift their winter ranges an average of 0.6 km away from a number of historic DWA in order to access cover and supplemental food at residential developments (Hurst and Porter 2008). Wintering area size of these deer was reduced by 50% as they concentrated their activity near residential homes. Further, deer in this study migrated directly to areas where supplemental food was provided in previous years, but these deer returned to their regular range when food was removed. These authors concluded that this loosely defined site-fidelity displayed around supplemental feeding sites may be important for allowing deer to shift their winter range over time, as the habitat changes or new resources become available.

However, it is unclear if deer that have been fed habitually over many years have the ability to display such plasticity in their winter habitat use. For example, it is largely unknown what happens to deer when supplemental food is removed from an area where generations of deer have learned to access supplemental food throughout winter. One would assume that deer would disperse into the nearest available cover, however, deer fed supplemental food continue to eat browse even when that food is provided *ad libitum* (Schmitz 1990, M. Tarr, personal observation). Further, if supplemental food is removed from an area, will deer learn to occupy a suitable DWA? Will forest stands suitable as DWAs be managed for such without evidence of deer occupation? And what happens to deer fed for years where current or historic DWAs don't exist nearby? Presumably winter mortality would be high during severe winters if these animals didn't have alternate, suitable habitats nearby.

Timber harvesting

Deer are known to shift their centers of activity to take advantage of emergency winter cuttings (Ozoga 1972) or to forage on tree tops in active logging sites located within or immediately adjacent to their wintering areas (Ozoga 1972, Tierson et al, 1985, St-Louis et al. 2000, Morrison et al. 2002, Morrison et al. 2003). In areas where winter conditions are moderate, deer have traveled 3.2 km outside of their normal winter range to access logging sites (Tierson et al. 1985). Gill (1957) reported that timber harvests in northern Maine would draw deer from 0.62 km or more, but it is unclear if these deer were moving outside of their regular DWA. In most cases, deer that move to logging sites outside of their normal range generally return to their regular range when this food source is exhausted (Tierson et al, 1985, St-Louis et al. 2000, Morrison et al. 2002, 2003). Timber harvesting within 1 km of wintering areas did not cause deer in New Brunswick to abandon their traditional winter range to access food (Boer 1992). Verme (1973) and Van Deelen et al. (1998) concluded that although deer may move to active logging operations to feed, deer fidelity to their DWA is probably strong enough to preclude total abandonment of one DWA for another.

The specific response of deer to timber harvesting is likely a function of the average winter severity. In areas where winter conditions are generally mild, some deer are remain on their summer range during winter and use active logging operations (Tierson et al. 1985); deer in Michigan spent the winter at an active logging job between their summer and winter range (Van Deelen et al. 1998). Non-migratory kin groups may develop and winter in patches of conifers within their summer range (Tierson et al. 1989) Timber harvesting that significantly increases the amount of browse in wintering areas could convert winter habitat into better summer range (MDIFW 1993) and potentially cause some deer to remain in their DWA year-round (Van Deelen 1999). However, deer fidelity to their summer range is generally stronger than it is to their DWA (Tierson et al. 1985, Aycrigg and Porter 1997, Van Deelen et al. 1998), and Tierson et al. (1985) observed no shift in deer summer range in response to logging.

When winter conditions are severe, no amount of food will support deer that don't have access to suitable cover (Gill 1957). Timber harvesting is an activity that can both accelerate and direct changes in forest structure, and this ultimately determines whether habitats will be suitable for deer (Boer 1992). In areas where winter is predictably severe, timber harvesting that removes a large proportion of the conifer cover or converts conifer stands to other forest types, is likely to be detrimental to deer (Gill 1957, Alexander and Garland 1985, Boer 1992, Maine 1993, Voigt et al. 1997, Van Deelen 1999, Potvin et al. 2003). On Anticosti Island aggressive harvesting of balsam fir has contributed to increasing the proportion of wintering areas comprised by white spruce, an inferior browse and cover species for deer (Potvin et al. 2003). In Maine, conversion of conifer stands to hardwood and mixedwood stands following timber harvesting is increasing the carrying capacity of deer summer range, but reducing the capacity of the winter range (MDIFW 2007).

In wintering areas where a large proportion of the conifer cover has been removed, deer mortality due to malnutrition and predation may increase (Banasiak 1961, MDIFW 1990) and deer productivity may decline (Verme 1977, 1979). In some cases, deer may return to a DWA for a number of years after conifer cover has been reduced, but in others, deer will readily move to better cover if winter conditions are severe (Gill 1957), even if that cover is less than optimal (Monthy 1984). DWAs that have been completely clear-cut are more likely to be abandoned by deer than those treated with partial timber harvests or no harvesting at all (Boer 1992). When conifer cover is removed it generally takes 30-40 years before the area will contain conifers large enough to provide functional winter cover for deer (Weber et al. 1983, Potvin and Boots 2004). Strong (1982) suggested that due to topography and growing conditions some DWAs are permanent, meaning that when these areas are cutover they aren't lost, but pass through successional stages that benefit other wildlife species before becoming optimal DWAs. However, in some areas (e.g., Maine), aggressive short-rotation timber harvesting is removing conifers from areas faster than they can grow to a size where they provide functional winter cover for deer (L. Kantar, personal communication).

Gill (1957) concluded that deer habit and trial-and-error selection of their DWAs makes it difficult to predict how deer will respond to timber harvesting. Boer (1992) suggested that deer should be expected to shift the location of their DWA over time in response to timber harvesting that affects cover and food availability. In general, timber harvesting that maintains or enhances the interspersion of functional conifer cover and abundant preferred browse is most likely to be beneficial to deer (Gill 1957, Verme 1973, Alexander and Garland 1985, Lavigne 1999, Voigt et al. 1997, Morrison et al. 2003).

CHAPTER III: MANAGEMENT OF DEER WINTERING AREAS

There are a number of themes that have long-been repeated to describe the conditions that make a given site "ideal" as a DWA. It is generally agreed that the ideal DWA is one where mature spruce-fir stands that provide functional winter shelter and habitats that provide abundant browse, are highly interspersed and connected by corridors of mature conifers that facilitate deer movement between all habitats under a variety of snow conditions (Gill 1957, Boer 1978, Weber et al. 1983, Alexander and Garland 1985, Voigt et al. 1997, Lavigne 1999, Morrison et al. 2003, Potvin and Boots 2004). In the ideal DWA, the proportion of habitats that provide either cover or food are balanced in relation to the average winter severity of an area (Gill 1957, NBDNR 2002, NSDNR 2004). In sites where winters are predictably severe, a greater proportion of the DWA is comprised of mature spruce-fir stands that provide cover. In areas where winter conditions are mild to moderate, a greater proportion of the DWA is comprised of habitats that provide abundant food. In both areas, once the minimum requirements for cover are met, food availability is maximized to ensure that deer are able to maintain a high level of energy intake even when weather conditions confine them to dense conifer cover. Conifer stands are managed to provide not only shelter, but to also maximize the availability of lichens and litterfall which serve as critical food when deer are confined to dense conifers. Finally, corridors of dense spruce-fir are maintained to ensure that deer are able to avoid predators and access suitable browse even when winter conditions are severe.

Four objectives for creating and maintaining an ideal DWA

From this basic description of the characteristics that define an ideal DWA, four overarching objectives can be identified which can serve as a guide when the primary management goal is to create and maintain ideal deer wintering habitat. They are:

- Maintain an adequate amount of functional conifer cover at all times.
- Perpetuate a constant, abundant supply of accessible, preferred food.
- Maintain a high level of interspersion of functional cover and accessible food.
- Maximize deer mobility between areas that provide functional cover and areas that provide food.

These four objectives for creating an ideal DWA are based directly on recommendations made by authors and deer biologists from across the spruce-fir-deer range including, Gill (1957), Verme (1965), Ozoga (1968), Drolet (1976), Boer (1978), Telfer (1978), Potvin and Huot (1983), Weber et al. (1983), Alexander and Garland (1985), Lavigne (1999), Reay et al. (1990), Lock (1997), Voigt et al. (1997), NBDNR (2002), and Morrison et al. (2003).

Manage DWAs at the landscape scale

These objectives are helpful for creating the best conditions possible on any ownership that contains some component of deer wintering habitat. However, they are most appropriate and best applied at a larger landscape scale where all of the winter habitat needs of deer can be met and perpetuated over time. Management at a larger scale, within a watershed for example (Boer 1992), allows managers to take advantage of natural growing conditions that dictate what sites are best suited for growing large, healthy spruce-fir trees; these sites become the focus for managing functional cover for deer. On sites where growing conditions dictate that spruce and fir will face heavy competition from hardwoods, such sites are managed primarily as hardwood or mixedwood browse areas. The natural constraints that determine where the best cover or browse should be located for deer also determine where the best forest products for any given trees species can be grown (Frank and Bjorkbom 1973, Reay et al. 1990). Spruce-fir stands that provide the highest value winter cover for deer often represent the highest value spruce-fir timber (Lavigne 1999). While this can lead to conflicts between timber and deer management objectives, managing at a larger scale provides flexibility in how forest stands within any area are utilized by deer and people, because the specific location of stands that provide either functional cover or browse doesn't need to be static. Instead, while the amount of cover and browse should always remain stable and in proper proportion for the area, commercial timber harvesting can be used as a viable tool for shifting the location of these resources throughout the area over time - as they do under natural conditions following disturbances (e.g., insects, wind/ice storm) and the predictable successional patterns of spruce-fir stands. Following this natural model, careful planning allows managers to maintain a perpetual shifting mosaic of mature conifer cover and browse to meet the winter habitat needs of deer across a working landscape. This means that all forest stands can be harvested over time and planned commercial timber harvests become the tool of choice for directing shifts in deer habitat in a predictable manner (Gill 1957, Boer 1978, Telfer 1978, Reay et al. 1990, NBDNR 2002).

Balancing DWA and timber management objectives

Developing plans for maintaining ideal DWAs is relatively easy on properties where deer habitat management is either the main objective (e.g., state-owned wildlife management area) or is mandated by contract (e.g., New Brunswick Crown Lands). Current habitat conditions are assessed, habitat needs are determined, and timber harvesting is prescribed specifically to improve or maintain habitat conditions for deer. However, in many areas, especially in New England states, the majority of the largest DWAs occur on private land where the main objective is commercial timber production, not deer habitat management (L. Kantar, personal communication; W. Staats, personal communication). In states like New Hampshire and Maine there is a historic, ongoing struggle by state wildlife agencies to convince commercial forest owners to alter their timber harvesting goals, to help accomplish agency goals for managing DWA (NHFG 1970, Lavigne 1999, C. Hulsey, personal communication; L. Kantar, personal communication; W. Staats, personal communication). While there are some success stories, few of these efforts have produced ideal DWAs because economic pressure to extract timber products thoroughly trumped the protection of DWAs for deer.

There are a number of reasons why efforts to accomplish deer habitat management objectives may fail on private land. Some are complex; for example, how do we accomplish long-term habitat management goals on private, commercial timberland that may change ownership as frequently as every 10 - 15 years? This is a real-world, common dilemma in northern New Hampshire and Maine, with no clear solution identified (Hagan et al. 2005, Fernholz et al. 2007, C. Hulsey, personal communication; W. Staats, personal communication). However, some of the failure may simply be due to miscommunication and/or lack of understanding about how to easily incorporate recommendations for improving DWAs into regular timber management prescriptions. Some successes have occurred when individual agency wildlife biologists have worked one-on-one with individual forest managers to plan and layout timber harvests in DWAs (C. Hulsey, personal communication; J. Pratte, personal communication; W. Staats, personal communication). Agency biologists can also meet directly with forest managers to review timber harvests planned in DWAs before they are implemented (NBDNR 2002). Conversely, harvest objectives may be determined by the landowner, not the forest manager and little cooperation can occur because objectives may be dictated by a lumber mill that requires a certain volume of wood, or a timber investment company that needs to generate investment returns (Hagan et al. 2005, Fernholz et al. 2007). These are actual examples from northern New England that identify that much of the land on which DWAs occur is owned for a reason that has nothing to do with deer. As such, attempts to incorporate deer habitat management goals on commercial forestland are likely to fail if those goals require a landowner to stray far from their original objectives and reasons for owning the land.

A more successful approach is to recognize the constraints under which managers of these lands work, and establish a goal of providing them with methods for accomplishing deer habitat improvement work as part of their regular efforts to manage forests. This approach has an established, successful model within the timber industry in Maine in the *Best Management Practices for Forestry: Protecting Maine's Water Quality* manual (DCMFS 2004). This manual provides practical, easy to understand, voluntary methods for avoiding impacts to water quality while harvesting timber. These techniques were developed cooperatively with public and industry foresters with input from a broad group of stakeholders interested in the management of Maine's forest resources. This manual was adapted and used successfully in New Hampshire as well (UNHCE 2005, S. Smith, personal communication). These manuals provide loggers and field foresters with the practical information they need to recognize and address potential water quality issues while they conduct their regular daily jobs planning and implementing timber harvests (S. Smith, personal communication).

A similar effort to develop best management practices (BMPs) for managing DWAs has been initiated recently by the MDIFW, Maine Forest Products Council, and the Small Woodlot Owner's Association of Maine (J. Pratte, personal communication), following a recommendation made by the Northern and Eastern Maine Deer Task Force (Martin 2007). The purpose of BMPs for DWAs is to educate landowners about what habitat elements comprise a functioning DWA, and to provide a variety of management guidelines that can be used to create or maintain those elements; landowners will ultimately decide how they can incorporate those guidelines into their forest management (J. Pratte, personal communication). To accomplish the goal of developing practical and effective BMPs, MDIFW will also conduct educational workshops for its staff, private foresters and loggers, and timberland owners to illustrate how DWA management can be accomplished through commercial timber harvesting (J. Pratte, personal communication).

Developing best management practices for DWAs

An important first step toward creating effective and practical BMPs for DWA management is educating wildlife biologists, foresters, and loggers in how traditional silviculture can be used to accomplish both timber and deer habitat management objectives. Silviculture consists of the various treatments that may be applied to forest stands to maintain or enhance their utility for any purpose (Smith 1986). When developing BMPs it is important to remember that there is no one "right" way to manage any parcel of land. Often what is "right" comes down to balancing landowner objectives (the purpose) with the capacity of the land to meet those objectives. The duties of the forester and wildlife biologist are then to analyze the natural and social factors bearing on each forest stand and devise and implement silvicultural treatments most appropriate to meet the identified objectives (Smith 1986). The major challenge in managing DWAs on private land is the social factor, namely, the often conflicting objectives of private landowners to harvest timber, and public value for high deer densities. Because the natural factors determining where the best timber products of any species can grow are the same factors determining where deer habitats comprised of the same timber species can be developed and maintained, the same silvicultural tools can be used to accomplish both public and private goals. How those tools are applied to accomplish both on the same parcel of land requires creativity and a little give-and-take on the part of both biologist and forester (C. Hulsey, personal communication). Deer managers who understand the silvicultural techniques for managing quality spruce-fir timber will be better prepared to work with forest managers to adapt those techniques in practical ways to manage DWAs. Forest managers who understand the components of an ideal DWA will be better prepared to recognize opportunities where they can adapt their regular silvicultural prescriptions to meet the habitat needs of deer, without straying far from their original timber management goals.

A critical challenge – with emphasis on northern Maine

The current situation in Maine presents an extreme challenge to agency biologists attempting to maintain DWAs on private land where spruce budworm and salvage harvesting has significantly reduced the amount of mature spruce-fir available to be managed as cover for deer (Lavigne 1999, MDIFW 2007). This situation is compounded by additional, ongoing reductions in the amount of mature spruce-fir as the result of intensive short-rotation commercial timber harvesting which is expected to continue at least into the near future (MDIFW 2007, C. Hulsey, personal communication, L. Kantar, personal communication, J. Pratt, personal communication). Of most importance, short-rotation harvesting reduces the absolute amount of mature spruce-fir stands that provide optimal cover, as well as reduces the length of time any stand provides the structural characteristics of a DWA. Repeated short-rotation timber harvesting across an entire DWA is not compatible with optimal long-term DWA management – there is no “magic bean” that will make such timber harvesting a viable tool for creating the type of structure deer require in areas where severe winter conditions force deer into dense conifer cover for extended periods. We are unaware of any scenario in which functioning DWAs can be successfully perpetuated in a landscape that lacks mature conifer stands as a regular component.

As such, owners of commercial timberland must make a conscious decision to identify areas where mature spruce-fir stands can be developed and perpetuated over time. Following the discussion above, these areas don’t need to be static, but can be shifted across the landscape to allow all areas to become available for harvest. In most situations these areas *should* shift across the landscape to ensure that conifer stands don't become over-mature and loose the structural characteristics that allow them to provide functional cover to deer. However, some mature conifer stands must be present at all times if DWA objectives are to be met, and suggestions will be provided to help managers determine how much cover is needed and how to ensure adequate cover is being maintained. On ownerships where mature conifer cover is currently lacking or absent, it may be necessary to defer timber harvesting in certain areas to allow such cover to develop. Harvesting may also need to be deferred or reduced initially in order to initiate stand conditions that can be perpetuated following the harvest rotations required to maintain functional winter cover for deer (described below). Such adjustments to harvest plans may very well result in economic loss to landowners and options for addressing this issue will be discussed. Voluntary agreements and land-use zoning that regulates timber harvesting within DWAs on private land offer some options to ensure that winter habitat needs of deer are met, but these vary in their efficacy to ensure the long-term viability of DWAs.

It is unclear how intensive, short-rotation timber harvesting influences deer occupation of historic DWAs and the ability of deer to locate and disperse into other cover when preferred cover is harvested. If required cover is removed and conifer stands are repeatedly harvested before they can provide functional cover for deer, deer should be expected to abandon the DWA (Gill 1957, Alexander and Garland 1985, Boer 1992, MDIFW 1993, Voigt et al. 1997, Van Deelen 1999, Potvin et al. 2003); where these deer go and how they survive severe winters is largely unknown. In landscapes where short-rotation harvesting maintains conifer cover below the minimum required by deer, deer populations goals will likely have to be adjusted to reflect the actual amount of habitat available, for as long as such harvesting continues.

Silvicultural tools for managing spruce-fir and DWAs

The main purpose of the following section is to illustrate how silvicultural techniques used to manage spruce-fir timber products can be used to create components of an ideal

DWA. This section is not intended to provide a thorough review of all of the silvicultural systems available to manage spruce-fir stands, but instead, introduces a few of the most common systems, when they are appropriate for managing spruce-fir timber, and how they can be applied to DWA management. There are a number of silvicultural guides available for managing spruce-fir forests (e.g., Frank and Bjorkbom 1973, Leak et al. 1987, OMNR 2000a, 2003) and these provide detailed instruction about how to apply the basic concepts introduced in this paper. Specific recommendations for managing deer habitat using silvicultural techniques are based on a thorough review of the deer literature and appropriate references are provided. This paper, and this chapter in particular, may prove useful to the Northern and Eastern Maine Deer Task Force as they develop BMPs for DWAs and subsequent educational outreach to landowners and natural resource professionals in Maine.

Where do spruce and fir grow?

Sites with growing conditions most favorable to spruce-fir trees are termed “primary” sites, and those less suited to growing spruce-fir are termed “secondary” sites (Frank and Bjorkbom 1973, Frank and Blum 1978, Reay et al. 1990). Primary spruce-fir sites are located in low, cool areas such as valley bottoms and at the toes of slopes, in areas where the topography is flat or gently sloping (Reay et al. 1990). Soils of these sites tend to be poorly-drained, silty or loamy, with high organic matter, and have a hardpan that restricts root growth just below the surface (Reay et al. 1990). Trees growing on primary sites tend to be shallow rooted and susceptible to windthrow (Frank and Bjorkbom 1973, Reay et al. 1990). Hardwoods such as paper birch, yellow birch, aspen, red maple, sugar maple, and beech are common but typically comprise less than 25% of these stands (Frank and Bjorkbom 1973).

Secondary spruce-fir sites occur on upper slopes, side hills, and ridges where the topography is gently rolling or sloping (Reay et al. 1990). Soils are well-drained, sandy or gravelly, and shallow to bedrock (Frank and Bjorkbom 1973, Reay et al. 1990). On secondary sites, hardwoods such as sugar maple, beech, and yellow birch often comprise 25-75% of the stand (Frank and Bjorkbom 1973).

Spruce and fir should generally be favored on primary sites because the growing conditions limit competition from the hardwoods and often produce poor-quality hardwood sawtimber (Frank and Bjorkbom 1973). These sites will, however, grow vigorous spruce and fir that can be valuable both as timber and winter cover for deer and some of the best cover in many DWAs occurs on primary sites (Gill 1957, NHFG 1970, Lavigne 1999). On secondary sites, the growth rates of spruce, fir, and hardwoods are similar and timber volume per acre can be increased by favoring conifers (Frank and Bjorkbom 1973, Leak et al. 1987). However, these sites are often capable of producing high-quality hardwood sawlogs and veneer logs (Frank and Bjorkbom 1973, Leak et al. 1987). Secondary sites in DWAs can be managed for cover, browse, or both depending on what forest products are favored in the stand.

Mixedwood stands occur on deep, well-drained, fertile soils on mid-slopes (OMNR 2003). These stands often originate on abandoned farmland or following disturbances such as fire, windthrow, insect damage, or logging that remove a large proportion of the overstory (Leak et al. 1987). Common species may include aspen, birch, spruce, fir, white pine, jack pine, red pine, white cedar, tamarack, balsam poplar (*P. balsamifera*), white elm (*Ulmus americana*), and black ash (*Fraxinus nigra*) (OMNR 2003). Early in their development, mixedwood stands are often comprised of aspen and white birch and in the absence of disturbance will convert to spruce and fir over time (OMNR 2003). Ground vegetation is usually abundant and diverse (OMNR 2003). These are complex forest stands that can be managed using a combination of traditional and non-traditional silviculture to produce high-quality timber products from a variety of tree species within the same stand (OMNR 2003). As such, mixwood stands are often best managed to provide deer with both cover and browse (Morrison et al. 2002). However, these stands provide a fair amount of flexibility in how they are managed for deer; if cover is lacking, the conifer component can be favored and the rotation length extended. If browse is lacking, hardwoods can be favored and managed with short-rotation harvests.

Spruce and fir are best grown on sites where shade from overstory trees reduces competition with ferns, raspberries, and shade-intolerant hardwoods during the initiation and seedling/sapling stage. However, spruce and fir can survive in the understory for many years and still respond well to release (OMNR 1998, Frank and Bjorkbom 1973). Balsam fir is the most shade tolerant, followed by red spruce which ranges from very tolerant to tolerant, followed by white spruce and black spruce which are both shade tolerant (Frank and Bjorkbom 1973). Regeneration of spruce-fir is dependent on seeds and is best when seeds fall on exposed mineral soil (Frank and Bjorkbom 1973, Reay et al. 1990). Significant seed production of spruce and fir may begin in trees as young as 10-15 years, but reaches its maximum in trees 25 years old (Frank and Bjorkbom 1973, OMNR 1998). The typical seed dispersal distance is about 40 m for balsam fir and black spruce, about 62 m for red spruce, and about 92 m for white spruce (Frank and Bjorkbom 1973). Harvests must take these distances into account to ensure successful spruce-fir regeneration. Spruce-fir seeds rarely remain viable in the soil for more than a single year (Frank and Bjorkbom 1973).

Rotation age of spruce and fir

Balsam fir reaches maturity at 60-80 years, and spruces 80-100 years (Frank and Bjorkbom 1973, Reay et al. 1990) Fir is typically grown to a maximum size of 25-30 cm in diameter at breast height (dbh) and is harvested for sawtimber or pulpwood (Frank and Bjorkbom 1973, Stadler 1987). Spruces are grown as large as 36-40 cm for pulpwood and 46-51 cm for sawlogs (Frank and Bjorkbom 1973, Stadler 1987). Typical rotation length is 60 years for balsam fir and 80-100 years for spruce (Reay et al. 1990). Balsam fir is often harvested well before it becomes over-mature due to its higher susceptibility to rot, spruce budworm, and BWA.

Silvicultural systems for managing spruce-fir forests

Silvicultural systems are a planned series of treatments that managers use during the entire life of a forest stand for the purpose of controlling establishment, species composition, and growth of the stand (OMNR 2000a). Spruce-fir timber stands are managed using uneven-aged or even-aged silvicultural systems. The following is a brief description of each system, how they are commonly used for managing timber, and examples of how they can be applied to manage DWAs.

Uneven-aged ("Selection") systems

Uneven-aged or "Selection" systems are used to manage spruce-fir stands in a manner that allows frequent harvests of high-value timber products (OMNR 2003, Frank and Blum 1978). This is accomplished by managing stands to ensure that there is always at least three distinct age-classes of trees within the stand (Frank and Bjorkbom 1973, Smith 1986). Once three age-classes are established, mature trees can be removed commercially about every 10 years (primary sites) to 20-25 years (secondary sites) (Frank and Bjorkbom 1973, Leak et al. 1987, Voigt et al. 1997). In the absence of timber harvesting, many spruce-fir forests naturally become uneven-aged, as shade tolerant spruce and fir are able to regenerate within the shade of these stands and are released when individual mature trees die and fall (Frank and Bjorkbom 1973).

At no time is the overstory completely removed when using selection systems; trees are removed individually ("single-tree selection") or in small groups ("group selection") (OMNR 2000a). By maintaining permanent forest cover while conducting partial timber harvests, selection systems are designed to favor trees that grow well in the shade (Leak et al. 1987, OMNR 2000a). Well-developed uneven-aged stands are comprised by trees that vary in height and diameter (Frank and Bjorkbom 1973).

Single-tree selection removes individual trees in a uniform manner throughout the stand and retains the highest level of crown closure of any of the silvicultural systems. More than 90% of the regeneration following single-tree selection will be spruce-fir and tolerant hardwoods such as beech (Leak et al. 1987). This system can be used to encourage the growth of high-value spruce-fir sawtimber.

Group-selection removes trees in groups ranging in size from 0.1-0.8 ha (Leak et al. 1987, Voigt et al. 1997). Smith (1986) considers the maximum appropriate size for group openings to be about twice the height of the surrounding mature trees. Groups at the larger end of the scale will encourage a greater mixture of intolerant hardwoods within the stand, while still favoring spruce and fir (Leak et al. 1987). Group-selection that just removes mature overstory trees can be used to release sapling- and pole-sized trees that can be developed into quality timber. Groups that remove all trees <5 cm will encourage more hardwoods, which has the added benefit of providing browse for deer. Group-selection can be especially useful for removing groups of diseased or over-mature trees from the stand (Leak et al. 1987)

Advantages of uneven-aged systems for producing timber

Selection silviculture has many advantages when it is used to manage timber:

- A constant supply of high-value timber products can be removed to provide steady revenue from each stand.
- Uneven-aged stands are far less susceptible to damage from spruce-budworm and balsam woolly adelgid because the entire stand never reaches maturity at the same time (Frank and Bjorkbom 1973, Whitter et al. 1984, K. Lombard, personal communication).
- Frequent timber harvests facilitate the regular removal of balsam fir to favor red spruce, which further improves the stand's resistance to insects (Frank and Bjorkbom 1973, Alexander and Garland 1985, Reay et al. 1990).
- Frequent harvests reduce the need for non-commercial timber stand improvement, because trees of all sizes can be removed during each harvest (Leak et al. 1987).
- Continuous overstory maintains a permanent seed source for natural regeneration of spruce-fir (OMNR 2000a).
- Selection systems can be less expensive than clearcutting or shelterwood systems if these require planting to regenerate spruce-fir (OMNR 2000a).

Disadvantages of uneven-aged systems for producing timber

- Compared to even-aged stands, uneven-aged stands are slower to operate because fewer trees are removed per acre. This means a larger area must be covered to harvest a given volume of wood.
- Harvesting in uneven-aged stands is also slower because operators must be careful to avoid damaging residual trees and regeneration (Frank and Bjorkbom 1973).

- Uneven-aged stands can be more expensive to harvest during a single-cutting cycle than even-aged stands.
- Uneven-aged systems are not generally acceptable to industrial forest landowners due to the disadvantages listed above (Stadler 1987).

Applying uneven-aged silviculture to DWA management

- Selection systems are the preferred way to manage the cover component of DWAs because they maintain the greatest amount of conifer crown closure while still allowing browse and conifers to be regenerated (Alexander and Garland 1985, Boer 1978, Reay et al. 1990, NBDNR 2002).
- Group-selection is preferred over single-tree selection because it retains denser pockets of cover while also promoting more browse for deer (Alexander and Garland 1985, Boer 1978, Reay et al. 1990, NBDNR 2002). Single-tree selection may impact a greater proportion of crown closure by being scattered uniformly across the stand.
    - Groups in stands managed for cover should be between 0.4-0.8 ha to provide the greatest amount of browse (Voigt et al. 1997).
    - Groups in known bedding areas and in travel corridors should be on the smaller end of the scale and designed to retain 80% crown closure at all times (OMNR 2005, Voigt et al. 1997).
    - Mature trees should be harvested every 10-20 years to perpetuate conifer cover and maximize the amount of browse available to deer within spruce-fir stands (Reay et al. 1990).
        - If harvesting with the shorter cutting cycle, group-selection may provide as much browse over time as heavier even-aged cutting (OMNR 2005) and it will generally provide a more stable supply of accessible browse.
    - Lichen and litterfall abundance is highest in uneven-aged stands (Lang et al. 1980), but lichen diversity may be lowest in dense conifers (Neitlich and McCune 1997). Larger groups that encourage hardwoods within

spruce-fir stands may maximize both lichen diversity and abundance (Neitlich and McCune 1997).

- In mixedwood stands, group-selection can be used to simultaneously increase browse availability and improve cover (Voigt et al. 1997, Morrison et al. 2002).
    - This can be accomplished by encouraging and retaining conifer patches that are at least 0.4 ha (20 m x 20 m), at least 10 m tall, and have at least 60% crown closure (OMNR 2005).
        - Use group-selection to create browse openings immediately adjacent to these conifer patches.
        - Use group-selection to remove hardwoods that are over-topping young conifers that can be developed into suitable cover patches and/or timber over time.
- The “strip-selection” method (Smith 1982), in which each age-class is concentrated in a long, narrow strip, rather than scattered uniformly throughout the stand, can be used to reduce many of the costs associated with uneven-aged systems while still maintaining some of the beneficial cover characteristics of uneven-aged stands.
    - This system differs from progressive strip clear-cutting or strip-shelterwood in that the objective is to maintain a minimum of three age-classes across the entire series of strips (Smith 1986).
        - This method more accurately describes what Marston (1986) and Stadler (1987) term “even-aged strip clear-cutting” to create the multi-aged DWA scenarios they recommend for managing spruce-fir DWAs in Maine.
    - Unlike other uneven-aged systems, the strip-selection method can be used on sites that are susceptible to windthrow by cutting strips progressively toward the prevailing wind.
- Frequent harvests in uneven-aged stands allow young trees to be thinned as part of the regular commercial harvest. Thinning increases the crown volume and growth of young trees which can reduce the age at which they can provide functional cover to deer (Reay et al. 1990).

Even-aged systems

The purpose of even-aged management is to create and maintain a stand where the difference in age between the youngest and oldest trees is no more than 10-20 years, or 25% of the rotation length (Frank and Bjorkbom 1973). Even-aged stands can often be recognized by the uniform height of their trees, though they are usually comprised of trees that may vary significantly in their diameter (Frank and Bjorkbom 1973). In nature, even-aged stands are initiated when a disturbance removes all or enough of the overstory to cause the entire stand to regenerate at approximately the same time. For example, large acreages of spruce-fir forests in Ontario and Maine regenerated in even-aged stands following the 1977-1988 spruce budworm outbreak that caused significant mortality to overstory spruce-fir (Lock 1997, Lavigne 1999).

In even-aged systems, the regeneration harvest removes all of the mature overstory trees either at once (clear-cut), or in two or more stages (shelterwood). Clear-cutting is most appropriate in stands that are susceptible to blow down and in those where advanced regeneration is present. If advanced regeneration is absent, a shelterwood is used to first establish the regeneration before the overstory is removed (Frank and Bjorkbom 1973).

Clear-cutting

Unless planting will immediately follow cutting, clear-cutting to regenerate spruce-fir is reserved primarily for stands that already contain advanced spruce-fir regeneration (Frank and Bjorkbom 1973, OMNR 2000a). The purpose of the silvicultural clear-cut is to completely remove the overstory to provide full sunlight to the advanced regeneration below. Therefore, all trees <5 cm in diameter should be removed from the stand in a single harvest (Frank and Bjorkbom 1973, Leak et al. 1987, NBDNR 2002). Clear-cutting is most appropriate in shallow-rooted, spruce-fir stands where leaving residual trees would likely result in significant loss from windthrow (Frank and Bjorkbom 1973, NBDNR 2002).

Strip clear-cutting

Strip clear-cutting removes the overstory in alternating strips, rather than in groups or blocks. It is desirable on sites where trees are shallow-rooted, but advanced regeneration is lacking (Leak et al. 1987, OMNR 2002). The width of the harvested strip depends on the tree species desired (Frank and Bjorkbom 1973, Leak et al. 1987, OMNR 2002). Strips cut to regenerate balsam fir and black spruce should be 50-70 m wide, those to regenerate red spruce and white spruce no more than about 120 m wide (Frank and Bjorkbom 1973). Unharvested strips should be at least 20 m wide to ensure the residual stand is wind-firm (Frank and Bjorkbom 1973). Residual strips are removed 3-10 years later once suitable regeneration is established (Frank and Bjorkbom 1973). Spruce-fir seedlings are considered established when they are 15-30 cm (Frank and Bjorkbom 1973) and hardwoods when they are 90-120 cm tall (Leak et al. 1987). Strip clear-cutting can be accomplished either through the "alternate-strip" method where the stand is clear-cut in two stages, or the "progressive-strip" method in which the entire stand is cut in three or more stages (Smith 1986). These methods differ from the "strip-selection" method in that all strips are cut within a short enough time period that after all cuttings are complete, the regenerating stand is even-aged.

Shelterwood methods

The shelterwood system removes the overstory in either two or three stages in order to establish advanced regeneration under the shelter of the residual trees (OMNR 2003). The first cut is the regeneration cut in which 30-80% of the crown closure is removed depending on what trees are to be regenerated (Frank and Bjorkbom 1973, Leak et al. 1987, OMNR 2003). Spruce-fir and tolerant hardwoods are favored when >50-80% of the crown closure is retained; pines and intolerant hardwoods such as red maple and birches are favored by retaining 30-50% crown closure (Leak et al. 1987). Residual trees should be wind-firm and be the most vigorous, high-quality trees in the stand as they will provide the seed source for the regeneration (Frank and Bjorkbom 1987, Leak et al. 1987, OMNR 2003). Once the regeneration is established, the remaining trees are removed in either one or two additional cuttings to provide full sunlight to the regeneration. There are a variety of shelterwood methods including "uniform shelterwood" in which the overstory is removed uniformly across the entire stand, strip-shelterwood in which the overstory is removed in stages but in strips, and group-shelterwood where the overstory is removed in groups or patches (Smith 1986).

Advantages of even-aged silviculture for producing timber

- Clear-cutting is the easiest silvicultural system to learn and apply.
- Clear-cutting is generally the easiest and least expensive system to operate with mechanized harvesting equipment.
    - All trees are removed at once so there is no concern about damage to a residual stand.
- Strip clear-cutting can be used in place of a shelterwood to establish natural regeneration on sites that are susceptible to windthrow.
- Shelterwood systems are more reliable than clear-cutting for establishing desirable regeneration.
    - Regeneration is usually more uniform in shelterwoods than in clear-cuts.
    - Compared to clear-cuts, shelterwoods allow better control over what species regenerate (OMNR 2000a).
    - Shelterwoods are ideal for growing high-value sawtimber in mixedwood stands (Leak et al. 1987).

Disadvantages of even-aged silviculture for producing timber

- Clear-cuts will not produce marketable wood for a long time after they are harvested.
- Clear-cuts require advanced regeneration to ensure desired species are present after the overstory is removed (if not planting).
- Competition from undesirable species, especially intolerant hardwoods, can be intense in clear-cuts.
- Shelterwoods require skill to prepare site for regeneration and to avoid damaging the residual stand.

  - These same factors also increase the costs of logging in shelterwoods compared to clear-cuts (OMNR 2003).
- Unlike in uneven-aged stands, intermediate cleanings and thinnings are expensive because they often aren't associated with commercial timber harvests.

Applying even-aged silviculture to manage conifer cover in DWAs

- Even-aged management is the least preferred alternative for managing cover in DWAs because it removes all or a large proportion of the cover at once (Reay et al. 1990, Voigt et al. 1997, NBDNR 2002).
  - Clear-cutting spruce-fir stands is suggested as appropriate only in DWAs >80 ha where other areas of suitable cover can be maintained while harvested stands regenerate (Reay et al. 1990, NHFSSWT 1997, NBDNR 2002).
  - Stadler (1987) suggested that clear-cuts should not exceed 2 ha in DWAs <160 ha; those in DWAs >160ha should not exceed 4 ha.
  - In wintering areas >100 km^2, clear-cuts as large as 30-60 ha can be used to regenerate cover, but no more than 30% of the DWA should be harvested before the cut areas have grown to 6 m in height (Voigt et al. 1997).
  - Clear-cutting is appropriate in mature and over-mature spruce-fir stands where crown volume is rapidly declining and expected within 5 years to fall below minimum levels required to provide functional cover (NBDNR 2002).
- Strip clear-cutting is preferred over clear-cutting and shelterwood systems for promoting the best interspersion of cover and browse (Gill 1957, Boer 1978, NBDNR 2002).
  - Recommendations for the width of strip cuts range from 6-60 m (Boer 1978, Alexander and Garland 1985, Reay et al. 1990, Voigt et al. 1997, NBDNR 2002). In most cases, following traditional silvicultural recommendations to regenerate the desired species from the adjacent uncut strips seems appropriate.

- Uncut strips can meet short-term needs for cover when they retain a high proportion of crown closure (NBDNR 2002).
  - When this is the objective, strip cuts should be no more than 30 m wide and uncut strips should be at least 50 m or twice the width of the cut strips, whichever is greater (NBDNR 2002).
  - These strips should be cut 10-15 years later (NBDNR 2002) or when the regeneration is 5-10 m tall and can intercept snow (Voigt et al. 1997).
  - Best cover will be retained if no more than 20% of the stand is cut during the first harvest (NBDNR 2002).
- In mixedwood stands where windthrow is a concern, strip cuts 9-16 m wide can be used perpetuate spruce-fir, especially if advanced regeneration is present before cutting (Leak et al. 1987). These softwood strips can improve deer access to browse within mixedwood stands, provide cover (Morrison et al. 2003), and be harvested for pulpwood or sawtimber at a later date.
- Orientation of strips should be perpendicular to prevailing winds to protect the residual stand and deer from wind (Alexander and Garland 1985, Leak et al. 1987).

- How to maintain cover when clearcutting is required to meet timber objectives:
  - Openings should be irregular in shape and separated by stands providing functional cover that are at least equal in size to the areas harvested (Boer 1978, NSDNR 2004).
  - Groups or strips of conifers should be left standing to improve deer access to browse.
    - Uncut patches should be as large as possible; conifer patches >2 ha were most likely to be used by deer in clear-cuts in (Monthy 1984).
    - Conifer patches should be at least 0.4 ha (20 m x 20 m), at least 10 m tall, and have at least 60% crown closure (OMNR 2005).

        - Patches as small as 3-5 conifers are better than no cover; trees in these patches should be at least 10 m tall, have interlocking crowns, and separated no more than 30-60 m from other patches. (Voigt et al. 1997, OMNR 2005).

Applying even-aged silviculture to promote browse in DWAs

- Clear-cutting is frequently prescribed as the preferred method for managing areas specifically dedicated to perpetuating browse (Gill 1957, Reay. et al. 1990, NHFSSWT 1997).
    - Clear-cuts from 0.2-10 ha (Boer 1978, Reay et al. 1990, Voigt et al. 1997) are regularly prescribed.
        - Many small openings scattered throughout the DWA are preferred over a few large openings (Telfer 1978).
        - Cuts on the large end of this scale are detrimental if conifers that allow deer to access food are removed (Voigt et al. 1997). Follow recommendations for maintaining cover in clear-cuts (above).
        - Cuts >0.8 ha are most likely to encourage intolerant hardwoods (Leak et al. 1987) which are browsed by deer.
    - Clear-cut size is probably less important than shape in determining value to deer:
        - Long, irregular strips <100 m wide are preferred because they provide greater interspersion of cover and food than do wide, square-shaped openings (Wetzel et al. 1975, Boer 1978, Telfer et al. 1978).
- Avoid treating all hardwood stands in one period in order to maintain browse production over time (NBDNR 2002).
    - At least 10% of the area should be regenerated every 10 years to maintain a stable supply of accessible browse (Reay et al. 1990).
- Clear-cuts, strip clear-cuts, and shelterwoods can be used to generate and perpetuate browse for deer in spruce-fir, hardwood, and mixedwood stands managed for high-value timber. Opening size and shape can be dictated by

silvicultural prescriptions for the specific timber species desired (Frank and Bjorkbom 1973, Leak et al. 1987, OMNR 2000a, 2003).

- Openings that reduce overstory crown closure to <50% will produce the greatest amount of browse.

Intermediate silvicultural treatments

In spruce-fir stands, intermediate “cleaning” and “thinning” treatments are often required to promote desirable growth and form of young trees being grown for timber. In uneven-aged stands, this work is conducted in an ongoing manner as part of regular commercial harvesting of mature trees. In even-aged stands, this work is conducted after the overstory has been removed and the regeneration is free to grow (Frank and Bjorkbom 1973). In most instances, cleaning and thinning in even-aged stands is conducted in non-commercial operations, but thinnings in the later stages of stand development may produce some small, merchantable trees (Frank and Bjorkbom 1973).

Cleaning

The purpose of cleaning or “tending”, is to remove hardwood or undesirable softwood species that are over-topping desirable spruce-fir regeneration (Leak et al. 1987, OMNR 2000) when the trees are no older than the sapling stage (Smith 1986). By removing hardwood competition, growth of future crop trees is enhanced by improving their crown formation and root development (Frank et al. 1973). A single cleaning conducted when spruce-fir regeneration is about 3-3.5 m tall is usually suitable to ensure that softwoods will remain dominant over hardwoods (Frank and Bjorkbom 1973). Hardwoods are typically removed by killing them with herbicides or by cutting with hand tools (Leak et al. 1987, Ontario 2000a). Cleanings can also be used in 10-20 year old mixedwood stands to shift the species composition in favor of softwoods (Leak et al. 1987)

Thinning

The main purpose of thinning is to shift the growth of the stand onto the crop trees and reduce the length of time required to grow these trees into high-value timber (Frank and Bjorkborn 1973). This is accomplished by removing trees which are in direct competition with future crop trees. The first thinning for timber production is usually conducted when regenerating trees are between 25-35 years old and is pre-commercial, meaning that no trees with any appreciable value are removed from the stand as part of this harvest (Frank and Bjorkbom 1973). Follow up thinnings may occur in 10-20 year intervals. By focusing tree removal on balsam fir, thinning can be used to further shift the composition of the stand to spruce (Frank and Bjorkbom 1973, Frank and Blum 1978, Reay et al. 1990). Thinnings conducted in the later stages of stand development may allow some revenue to be captured from trees that would normally be lost due to natural thinning of the stand (Frank and Bjorkbom 1973).

Site preparation

Successfully regenerating spruce-fir in clearcuts and shelterwoods often requires site preparation that scarifies the top 5-8 cm of the soil to provide a favorable seed bed (Frank and Bjorkbom 1973, OMNR 1998). Scarification favors spruce, hemlock, and cedar, which are all desirable winter cover species for deer, but can encourage competition from raspberries and hardwoods (NBDNR 2002).

Planting

On sites where natural regeneration of spruce-fir is inadequate, it may be necessary to plant seedlings. Spruce is generally recommended for planting over fir because it is much less palatable to deer and less susceptible to insects (Gill 1957, Telfer 1978). If fir is planted in areas with high deer density it may be necessary to temporarily fence the plantings to protect them from deer browsing (Potvin et al. 2000). Planting is expensive and time consuming so methods that encourage natural regeneration are favored whenever possible (OMNR 2000a).

Improving deer habitat with intermediate silvicultural treatments

- Cleaning should only be conducted after hardwoods have grown >2 m in height and are no longer accessible as browse.

  - If cleaning operations need to occur sooner, spread them throughout the DWA and over a series of years to reduce the impact to browse availability during any year or in any portion of the DWA (OMNR 2005).
- Thinning promotes stands comprised of trees with wide, deep crowns that are capable of providing superior cover at an earlier age than non-thinned stands (Telfer 1978, Reay et al. 1990, NBDNR 2002).
  - The rule of thumb is to thin early or not at all; thinning should be conducted early in the rotation when tree height and crown size is insufficient to provide cover; thinning should never reduce shelter, it should encourage cover to develop quicker (Reay et al. 1990).
    - Thin even-aged stands or patches of spruce-fir regeneration in uneven-aged stands before trees are 4.5 m tall or before mean stand diameter reaches 5.1 cm (Reay et al. 1990).
    - Thinning should be heavy or frequent enough that it won't be needed when the stand reaches the larger pole stage; thinning these stands will reduce cover (Reay et al. 1990).
      - The goal is to maintain stocking that will achieve minimum functional crown closure for cover by one half of the rotation (Reay et al. 1990).
- Thinning improves tree vigor which reduces stand susceptibility to insects and disease.
  - Thinning can focus on removing fir in areas where risk of BWA is high.
  - Fir, hemlock, and cedar are capable of developing deep crowns that provide superior cover compared to other conifers, so it may not always be best to favor spruce (Telfer 1978, W. Staats, personal communication).
  - Don't thin spruce-fir stands comprised of trees with a live-crown ratio <30% or those with <6 growth rings per cm as thinning will likely cause these stands to decline (Reay et al. 1990).
- Thinned stands may have greater litterfall and lichen diversity and abundance than non-thinned stands

  - Live branches support more lichens than dead ones; thinning increases live crown volume and live branch retention which may provide lichens a longer period of time to accumulate (Neitlich and McCune 1997).
- Commercial thinning of larger stands can maintain cover by reducing self-pruning of spruce-fir trees (NBDNR 2002).
  - Commercial thinning should not reduce crown closure below minimum functional levels (Reay et al. 1990, NBDNR 2002).
- Planting may be necessary where natural regeneration is inadequate to develop functional conifer cover in a reasonable time (NBDNR 2002).
  - Planting in DWAs should be limited to red and white spruce that are not palatable to deer (Gill 1957, NBDNR 2002).
  - Silvicultural treatments that promote natural regeneration should be used whenever possible (NBDNR 2002).

Timing of cutting

Winter is generally the best season to harvest timber in DWAs (Gill 1957, Telfer 1978, Alexander and Garland 1985, NHFSSWT 1997, St-Loius et al. 2000). Deer readily forage on tops of fallen trees and litterfall within active logging sites (Gill, 1957, Ozoga 1972, Tierson et al, 1985, St-Louis et al. 2000, Morrison et al. 2002, 2003), and skid trails and haul roads improve deer mobility and access to forage (Gill 1957, Alexander and Garland 1985). Winter logging often stimulates the best sprouting response from cut hardwoods (Reay et al. 1990). Further, deep snow is helpful for protecting advanced spruce-fir regeneration from logging damage (OMNR 2000a).

Summer logging is preferred whenever the goal is to establish spruce-fir regeneration because the best regeneration will occur on seed beds where mineral soil is scarified and exposed (Frank and Bjorkbom 1973, Reay et al. 1990). Clear-cutting aspen stands in early-summer can reduce aspen spouting and encourage more preferred browse species and forbs for deer (Wetzel et al. 1975). Deer don’t seem to prefer freshly cut twigs in active logging jobs compared to those cut earlier in winter; tops cut during logging in early or late-winter when shallow snow facilitates logging will still be used by deer (St-

Louis et al. 2000). Browse provided from the tops of harvested trees is probably most beneficial to deer anytime that access to other foods is limited by deep snow.

Maintaining an ideal DWA on commercial timberland

> *"You cannot will a particular area to be a deer yard no matter how hard you try. If the deer are telling you a site meets their minimum winter requirements by their presence, go with it. In this matter, deer know more than biologists and probably foresters too."* (Alexander and Garland 1985)

To accomplish the first objective toward creating an ideal DWA – "Maintain an adequate amount of functional conifer cover at all times" – biologists and foresters first need to answer three important questions:

- What exactly *is* functional cover?
- What exactly is an *adequate amount* of functional cover?
- How do managers ensure an adequate amount of cover is being maintained?

<u>What is functional cover?</u>

Tree species, tree height, and percent stand crown closure are the main factors under the forest manager's control that determine if a forest stand can provide functional cover for deer. There is general consensus that conifer-dominated stands at least 10 m tall are capable of intercepting snow and providing cover for deer. However, there is less agreement on how much crown closure is required or needed. In areas where winter conditions are predictably moderate to severe, recommendations for conifer crown closure vary across the range and include recommendations for at least 50% (Maine Lavigne 1999; New Brunswick, NBDNR 2002; Nova Scotia, NSDNR 2004), and 70% (Vermont, Reay et al. 1990; Maine, Marston 1982, Stadler 1987). Recommending that managers provide crown closure somewhere between 50-70% may not provide enough guidance to plan timber harvests across an area as large as the spruce-fir range where winter conditions and deer habitat needs vary considerably.

More cover isn't always better. In DWAs where deer are limited by food availability, increasing the cover component may cause deer populations to plateau or decline (Potvin and Boots 2004). In these situations it might be more appropriate to manage for less crown closure or less mature conifer cover to increase accessible browse. Further, a harvest strategy that increases the amount of land managed in long-rotation for cover reduces the amount of land for other shorter-rotation timber products. Maintaining the minimum amount of conifer cover needed to meet DWA objectives, while maximizing the amount of area managed for browse and other timber products will allow for balance between DWA and timber management on the same property.

Winter severity and the tree species that comprise a conifer stand influence how dense the stand must be to provide functional cover. Mature stands comprised mostly of hemlock and cedar may provide functional cover with less crown closure than stands dominated by fir. Likewise, fir stands require less crown closure than those dominated by spruce. In very northern areas where winters are regularly severe, it may be appropriate to recommend crown closure as high as 70% (Marston 1982, Stadler 1987, Reay et al. 1990), while at middle latitudes of the range, where winter is consistently moderate-severe, crown closure closer to 50% may be appropriate (Lavigne 1999, NBDNR 2002). In southern New Brunswick and southeastern Nova Scotia where winters are mild-moderate and deer rarely require dense conifer cover, mature stands with conifers at least 10 m tall and with at least 30% crown closure are considered functional (NBDNR 2002, NSDNR 2004).

Many suggest that average winter severity should be used as a guide to determine what qualifies as functional cover (e.g., Gill 1957, NBDNR 2002, NSDNR 2004). Many states and provinces recognize that yarding behavior and DWA use in northern areas differ from those in southern areas due to predictable differences in winter severity (e.g., Maine, New Hampshire, Michigan, Minnesota, Ontario). New Brunswick makes different recommendations for what qualifies as minimum functional cover to account for this variability in northern and southern regions. Nova Scotia is considering the same recommendations. One potential benefit of this approach is the flexibility in how

commercial timberland can be managed across a large province (or state) where cover requirements vary. Specifically, landowners in southern areas might not need to manage for the same amount of cover as those in northern areas to meet DWA objectives.
New Brunswick manages for two different winter habitat types, Severe Winter Deer Habitat (SWDH) and Moderate Winter Deer Habitat (MWDH). Each defines functional cover differently in order to provide the best balance of functional cover, browse availability, and timber management opportunities across an area where winter conditions vary from moderate to severe. Specifically, these habitats are defined as:

"Severe Winter Deer Habitats" (SWDH)

- Mature conifer-dominated stands comprised of conifers at least 18 cm dbh, at least 10 m tall, and with at least 50% crown closure.
- Patches must be at least 10 ha in size and at least 300 m wide.
- At least 10% of the area within cover patches must be maintained to provide accessible browse.

"Moderate Winter Deer Habitats" (MDWH)

- Patches of mature conifer- or hardwood-conifer dominated stands comprised of conifers at least 18 cm dbh, at least 10 m tall, and with at least 30% crown closure.
- Patches must be at least 5 ha in size and at least 150 m wide.
- At least 30% of the area within patches must be maintained to provide accessible browse.

To apply these different habitat requirements, New Brunswick divides its province into two distinct winter severity regions: a Northern (severe winter) region where SWDH is the primary habitat managers must maintain, and a Southern (moderate winter) region where MWDH is the primary habitat that must be maintained (NBDNR 2002). New Brunswick requires that both habitat types be provided on provincial lands within each region to account for annual variability in winter conditions and habitat needs of deer.

Using snow depth to define severe and moderate winter areas in Maine

In order for government agencies or individual managers to apply the approach used in New Brunswick, there must be an effective way to delineate areas of severe and moderate winter. Snow depth is the main factor influencing occupations of DWAs and snow >40-50 cm confines deer to dense conifer cover. New Brunswick separated regions by the number of days with snow depth >50 cm and the frequency of such conditions in a 10 year period (R. Cumberland, personal communication). Nova Scotia attempted use snow depth >50 cm to delineate regions of severe and moderate winter but found that snow depth was too variable; most areas of the province routinely had snow >20 cm, that caused deer to migrate to DWA, but only a few specific sites had depths >50 cm. Analysis of average annual snow depth conducted across a large portion of the spruce-fir range is likely to reveal similar results to those in Nova Scotia. However, it would be valuable to investigate the relationship between snow depth >40-50 cm and local/regional use of DWAs.

In Maine, areas where snow depth typically is >50 cm roughly corresponds to the southern edge of the Northern and Eastern Wildlife Management Districts (WMD) where average winter severity is severe-very severe (Fig. 3, 4). This line might be appropriate to delineate a northern "severe winter" zone where crown closure in DWAs should be 50-70%, and a southern "moderate winter" zone where crown closure should be 30-50%.

Using WSI scores to define areas of severe and moderate winter in Maine

Perhaps a better variable to identify regions of winter severity is WSI scores because of historic data sets and ongoing efforts to measure WSI. For example, average WSI for each WMD in Maine has already been ranked as mild-very severe based on WSI scores collected in 1973-1998 (see Table 1, Lavigne 1999). This ranking could be used to identify two winter severity regions in Maine; a "severe" winter region comprised of WMDs with average WSI scores of ≥75, and a "moderate" winter region comprised by WMDs with scores <75. Following this approach, recommended crown closure within the severe region might be 70% and that in the moderate region might be 50%.

Reflection of a broader range of winter conditions might include three winter severity zones. For example, in WMDs where WSI scores are ≥75 (severe), conifer crown closure must be at least 70%; in WMDs where WSI scores are 60-74 (moderate), conifer crown

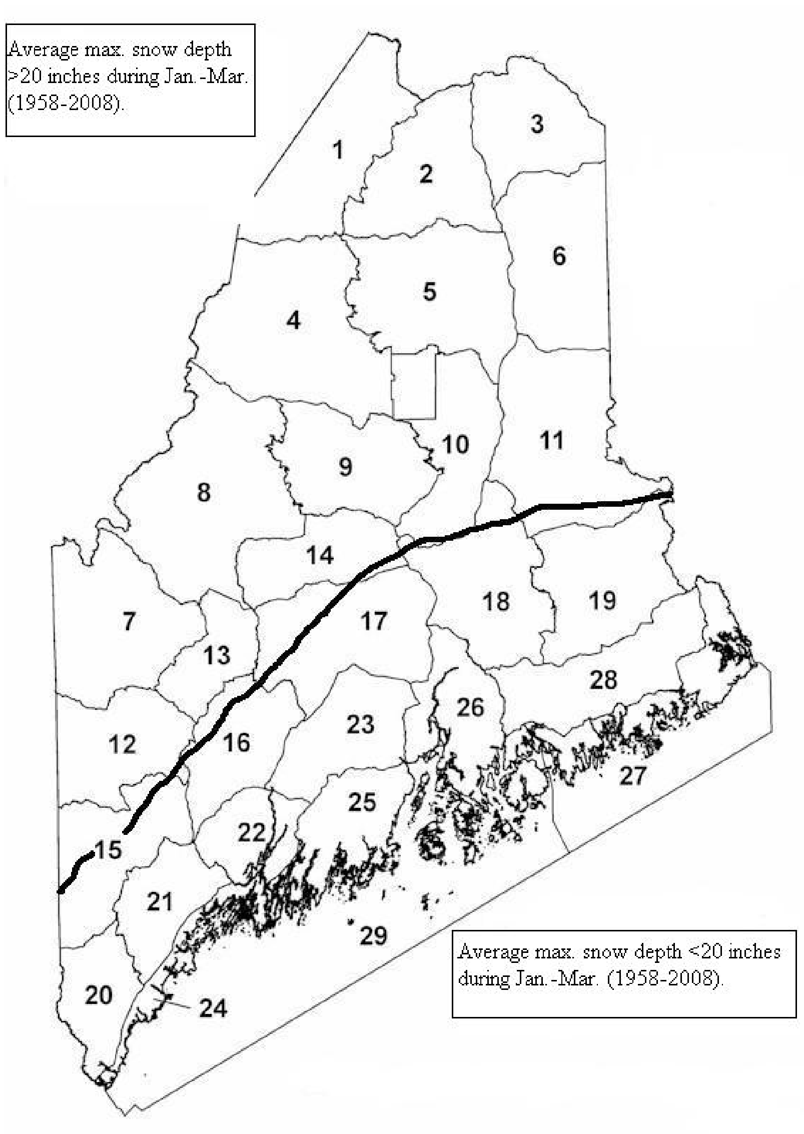

Figure 3. The line on the map delineates two regions in Maine that have average maximum snow depth of < and >20 inches (50 cm) in January-March. This line was created from 50 years (1958-2008) of the monthly average maximum snow depth measured at 96 weather stations located throughout Maine. Data are from the NOAA website (http://cdo.ncdc.noaa.gov/CDO/cdo); not every station had 50 years of data.

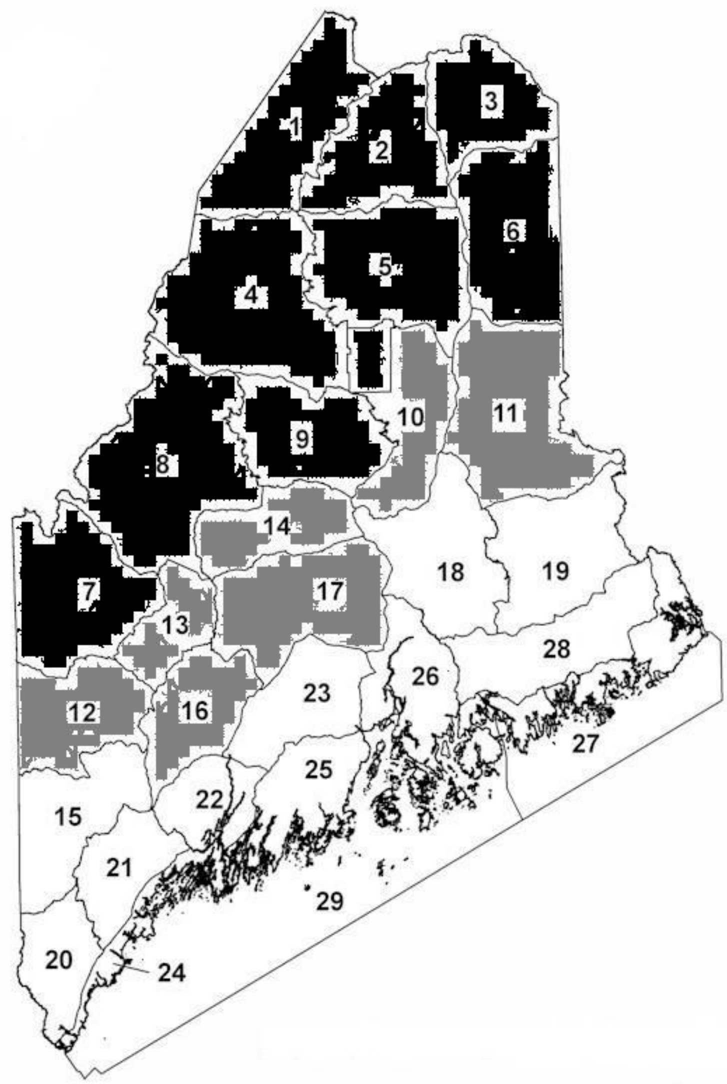

Figure 4. This figure identifies the relative winter severity index (average from 1973-1998) in Wildlife Management Districts in Maine. Severity was defined as severe-very severe (black), moderate (gray), and mild (white) based on descriptions and data from Lavigne (1999).

closure must be at least 50%, and in WMDs where WSI is <60, conifer crown closure must be at least 30% (Fig. 4). This approach would maintain suitable habitat for deer during typical winter conditions, afford some buffer in areas where conditions are variable, and allow managers the greatest flexibility in addressing DWA and timber production.

How small can a conifer stand be and still provide functional cover?

This question remains largely unanswered, but is frequently asked by land managers attempting to balance the needs of deer with timber harvesting goals. Again, tree species composition, crown closure, and perimeter-to-area ratio of mature stands are important; however, determining what deer truly need cover *from* is probably the most important variable. If the main function of dense conifers is to improve deer access to browse or lichens and litterfall, than stands can probably be relatively small (e.g., 2-5 ha; Monthy 1984, NBDNR 2002) and still remain functional. In fact, patches as small as 3-5 conifer trees (Voigt et al. 1997), or even single conifer trees can improve deer access to browse when snow conditions aren't restrictive (NHFSSWT 1997). However, if deer require cover from wind, stand size likely needs to be larger and probably needs to increase in some proportion to a decrease in both crown closure and patch width. As stand size and width decreases it probably makes sense to increase the amount of conifer cover in the 3-6 m level to provide deer the best protection from wind (Telfer 1978, Reay 2000). Finally, in areas where deer are subject to coyote and wolf predation, the importance of maintaining larger stands and maintaining stable connections between those stands may be especially important (Messier and Barrette 1985, MDIFW 2007).

Apply cover requirements consistently within specified regions

The decision for what qualifies as minimum functional cover should be determined by local/regional biologists who are best able to assess habitat needs of local deer populations and prescribe specific management recommendations to develop or maintain stands with the characteristics that meet the DWA needs of deer. Ideally, decisions for what qualifies for minimum functional cover should be clearly identified in writing, made available to the public, and applied consistently within well defined regions (e.g., WMD).

This approach reduces the chance of ambiguity or inconsistency of what is expected or required of landowners within one WMD.

Maintaining an adequate amount of functional cover

The most common recommendation is to maintain at least 50-60% of a DWA as functional cover at all times (Boer 1978, Stadler 1987, Reay et al. 1990, NHFSSWT 1997). New Brunswick and Nova Scotia require at least 75% of a DWA be maintained as priority deer habitat for each winter severity region (NBDNR 2002, NSDNR 2004). The remainder of a DWA should provide a regular source of browse which is easily produced as a by-product of timber harvests. Browse can be produced in hardwood and mixwood stands, as well as within regenerating conifer stands managed for timber and future winter shelter.

Maintain adequate conifer cover at all times using “area regulation”

“Area regulation” is one method for ensuring that the proper proportion of functional cover is maintained at all times. It is especially useful to maintain adequate cover in DWAs where commercial timber harvesting employs even-aged silviculture, since regenerating stands provide no immediate cover value to deer. Described by Reay et al. (1990), area regulation allows managers to calculate the specific proportion of each stand that should be regenerated during each harvest. In order to maintain at least 50% of the DWA in functional cover, the amount of area to be regenerated is determined by dividing the cutting interval of the stand by the rotation age. For example, in an uneven-aged spruce-fir stand with a rotation age of 100 years and a cutting interval of every 10 years, 10% of the stand (i.e., 10/100) should be regenerated during each entry into the stand. If the area regenerated exceeds the goal, than the amount of functional cover falls below the minimum required by deer; if the area regenerated is consistently less than the goal, than the area regenerated may be too small to ensure that future cover needs are met (Reay et al. 1990). Not using area regulation to regenerate stands on a scheduled rotation can result in a “boom and bust” situation where either excessive or too little cover exists (Boer 1982, Lavigne 1999, W. Staats, personal communication). Vermont and New Hampshire both use area regulation to plan timber harvests in DWAs.

Maintain adequate cover by manipulating rotation length and cutting interval

Stadler (1987) provides a very practical explanation for how rotation length and cutting cycle in spruce-fir stands can be manipulated to ensure that a minimum amount of conifer cover is always available to deer. He suggests that managing stands on a 75 year rotation and 15 year cutting cycle provides the best opportunity to maintain functional cover on at least 50% of a property, while still allowing landowners to meet their timber harvest objectives. Stands managed with these intervals are managed in concert with uneven-aged management of riparian, coniferous travel corridors to ensure that 50% of a DWA is maintained as functional shelter (Stadler 1987).

Plan locations of cover, browse, and timber over 80-100 year periods

Ideally, the specific locations and amount of area comprised of functional cover and accessible browse should be identified and forecast for the wintering area in a management plan covering at least an 80-100 year period (NBDNR 2002). Planning at this time scale is helpful for recognizing that many areas which currently meet DWA requirements may not necessarily be the same areas where future needs are met due to timber harvesting, natural stand maturation, or both (Boer 1992, OMNR 2005). Maps of existing locations of cover, browse, and travel corridors should be developed, along with maps that anticipate where these features will be maintained in the future (Telfer 1978, Monthy 1984, Boer 1992), and where they will be available in a variety of snow conditions (Morrison et al. 2002). New Brunswick and Nova Scotia require/recommend mapping these features a minimum of 20-25 years into the future (NBDNR 2002, OMNR 2005); mapping or assessing conditions and use of DWAs should occur prior to timber harvests. Boer (1992) suggested that mapping intervals longer than 5-10 years may miss areas that deer have abandoned and these areas may be needlessly excluded from timber harvesting. Likewise, deer may occupy new DWAs thereby requiring adjustment to planned timber harvests. Mapping DWAs and related habitats allows managers to determine the juxtaposition of cover, browse, and travel corridors, and to predict how timber harvests might improve or harm resources and functions of a DWA (Telfer 1978).

Suggestions for locating and managing cover, food, and travel corridors

The following provides additional guidance to assist planning and managing for long-term DWAs with functional cover, browse, and travel corridors.

Cooperation to manage at largest scale possible

Whenever possible, neighboring landowners should cooperatively manage DWAs that encompass multiple ownerships. Ideally, timber harvests would be conducted in a cooperative, coordinated manner to produce the most ideal arrangement of cover, food, and connections across the entire DWA (NSDNR 2004). When not possible or feasible, managers should at least assess their property in context with the surrounding land (Gill 1957). Communication by agency biologists is essential in this effort to help guide coordinated management of DWAs across multiple ownerships.

Enlarge existing DWAs when possible

Deer are reluctant to leave their DWA, but often shift their winter range over time to exploit better food and cover resources (Boer 1992, Hurst and Porter 2008). When planning habitat improvement work (within or across property boundaries), priority for enlarging or improving an existing DWA is recommended, rather than "creating" a new unoccupied DWA (Gill 1957, Beier and McCullough 1990).

Identify where cover will be managed over time

Managers should first determine where functional cover will be maintained over time, because stands that meet cover requirements must be mature and require most time to develop. This is especially true if even-aged silviculture is used to manage timber and cover simultaneously. In most cases, clear-cut stands must be at least 30-40 years old before they have cover value for deer (Weber et al. 1983, Voigt et al. 1997). As such, the best sites for perpetuating functional cover will generally be those that are capable of growing valuable spruce-fir sawtimber. Here, silvicultural recommendations for maintaining cover are most likely similar to those used for managing sawtimber. Further, landowners are more likely to invest resources for intermediate stand improvements that improve timber quality and accelerate the development of functional cover.

A minimum of 4-6 forest age-classes should be maintained within a DWA to ensure that a constant supply of cover and browse is maintained if timber is harvested continually (Boer 1978). Marston (1986) recommended maintaining 10 age-classes in a DWA managed on a 100-year rotation with 10-year cutting cycles when using even-aged silviculture. If stands are managed by area regulation, new forest stands will begin to provide functional cover as older stands are harvested. Maintaining a diverse forest age structure also protects the DWA from large-scale losses of cover from insect and disease damage.

Most cover stands should be harvested before the dominant trees become over-mature and begin to die. Allowing stands to become over-mature reduces both their timber and cover value, increases their susceptibility to insects and disease, and can make it difficult to establish natural regeneration to replace the stand. Over-mature or diseased stands should be the first stands harvested and scheduled for regeneration (Boer 1978, Marston 1982, Reay et al. 1990, NSDNR 2004). Long-term planning and use of area regulation will ensure functional cover is maintained and all stands are harvested before becoming over-mature.

On most commercial forestland, functional cover will be easiest to prescribe and maintain within riparian corridors where timber harvesting is already restricted or where BMPs are employed to avoid water quality impacts (Gill 1957, Telfer 1978, Monthy 1984, Reay et al. 1990, NHFSSWT 1997). Historically, riparian areas have been managed as the nucleus of DWAs on commercial forests in the northeastern U.S. (Gill 1957, NHFG 1970, Lavigne 1999). Travel corridors in riparian areas can be established permanently, or relocated as needed (Reay et al. 1990). However, if timber harvesting is completely restricted within these areas, aging and breakdown may reduce the cover value; in these cases, it might help to establish alternate travel lanes that are perpetuated by timber harvest.

Patches of functional cover and browse should be connected at all times with strips of conifer cover that facilitate deer movement. These strips should be 30-90 m wide (Boer

1978, Alexander and Garland 1985, Reay et al. 1990) and managed with uneven-aged silviculture to maintain 50-80% crown closure (NSDNR 2004, Voigt et al. 1997). Travel corridors should be integrated with riparian buffer strips whenever possible (Stadler 1987, Reay et al. 1990, NHFSSWT 1997).

Mixed wood stands surrounding riparian travel corridors and other primary spruce-fir sites can also be included to provide functional cover on sites where quality spruce-fir sawtimber is grown. Otherwise, mixedwood stands are probably best reserved for growing high-value hardwood timber or shorter-rotation timber products. Patches of conifers should be maintained within these stands primarily to improve access to browse.

Locating browse

Once the current and future locations of functional cover and travel corridors are identified, timber harvesting should be used to maintain a shifting mosaic of abundant, accessible browse around these habitats (OMNR 2005). Any stands not identified for meeting immediate or short-term cover needs can be harvested to increase food supply (OMNR 2005). Individual stands can be managed specifically to produce browse, or browse can be produced and maintained as a regular by-product of timber management. Hardwood stands, mixedwood stands, and secondary spruce-fir sites generally provide the best opportunity to manage browse through even-aged silviculture without causing any significant reduction in the short-term supply of cover.

Group-cuts created while removing timber in uneven-aged conifer stands can provide important browse for deer when deep snow confines them to dense conifer cover. However, browse should always be made available throughout the DWA. Browse located away from dense conifer cover is often used by deer in early winter when they first enter a DWA, and during mid-winter when snow conditions don't restrict deer to dense cover. Browse in these areas helps deer enter winter in better physical condition, provides access to food if they are caught outside the DWA in deep snow, and helps prolong availability of browse in dense conifer cover critical in periods of deep snow (Morrison et al. 1990).

Reay et al. (1990) and the NHFSSWT (1997) recommend that all commercial land immediately surrounding DWAs be managed to provide a constant supply of browse.

Optimum browse production can be maintained by managing browse on a 40 year rotation, where 25% of the area is regenerated every 10 years (Reay et al. 1990, NHFSSWT 1997, MNDNR 1986). If this is not possible, at least some browse cutting should be conducted every 10 years to ensure there is a constant supply of accessible browse (Reay et al. 1990, NHFSSWT 1997, Voigt et al. 1997). Efforts should be made to locate browse openings in areas where growing conditions favor regeneration of browse species preferred by deer in the area.

Some authors and states recommend managing a browse buffer strip at least 61.5 m wide around the entire perimeter of a DWA; this buffer should be managed by clear-cutting 1-5 acre blocks using a 40-year rotation and 10-year cutting cycle (MNDNR 1986, Reay et al. 1990, NHFSSWT 1997). To ensure browse is accessible, browse cuts should be made within 30 m of suitable cover in areas where snow depths exceed 50 cm and within 100 m of cover where snow depth is less (Voigt et al. 1997).

Lichen and litterfall abundance greatest in over-mature stands?

More research is needed to determine what stand conditions generate the highest litterfall and lichen production to benefit deer. Lichen litterfall increases linearly in fir stands 25-80 years of age; however, lichen litterfall may continue to increase for as many as 30 more years as lichens fall with branches and boles of dying trees (Lang et al. 1980). Further, lichen diversity is highest in conifer stands that have hardwood inclusions as large as 1000 m^2 (Neitlich and McCune 1997). Since lichens and litterfall likely improve forage intake rate when deer are confined to dense conifer cover, it would be valuable to know how lichen litterfall is related to different proportions of over-mature trees in conifer stands. Specifically, is there some proportion of over-mature trees that could be retained to improve lichen availability, without significantly increasing the stand's susceptibility to insects and diseases? Also, do deer eat lichens species that grow on hardwoods? If so, what is the ideal size of hardwood inclusions that will maximize lichen availability without reducing the cover value of conifer stands?

Manage spring and fall food sources

Hard mast from oak and beech trees help deer to efficiently accumulate fat reserves critical for winter survival. These foods are also important in early spring to help deer recover from winter malnutrition prior to spring green-up. Whenever possible, timber harvests should be used to improve mast production in hardwood stands within 1-2 km of DWAs (Voigt et al. 1997). Healthy dominant and co-dominant oaks and beech with well-rounded crowns should be released by removing competitors on at least 3-4 sides to improve mast production.

Openings planted with cool-season forages should be promoted near DWAs to provide high quality spring food to deer leaving a DWA (MNDNR 1986, OMNR 2005). Further, it would be valuable to determine if food plots planted with *Brassica* spp. (e.g., turnips, kale, rape) could be used in a cost-effective manner to improve the over-winter nutrition and survival of local deer herds suffering from low productivity.

Regulation, incentives, and other approaches for managing DWAs

Perpetuating cover and browse in DWAs can often be accomplished through existing plans to harvest timber. Biologists can assist timber managers to identify how plans to harvest, regenerate, tend, and thin forest stands will influence the availability and location of browse, cover, and travel corridors over time. If existing plans are the most efficient and effective way for the landowner to accomplish their objectives, than deviations from that plan for the purposes of managing DWAs should be avoided whenever possible. Instead, biologists should look for opportunities where cutting practices can be adjusted to allow the landowner to meet their objectives, while simultaneously providing more benefit to deer. However, there are times when significant deviations from a landowner's objectives must be made to best manage DWAs. Given that many landowners are unwilling to voluntarily adopt DWA objectives that conflict with their primary goals, a variety of regulations, incentives, and other approaches have been used in an attempt to maintain functioning DWAs on commercial forestland.

Protecting DWAs by land-use regulation

Vermont and Maine are the only states that afford specific protection to DWAs through land-use zoning or regulation. The following is a brief overview of specific programs within each state:

Vermont's Act 250

The state of Vermont has the Land Use and Development Law – Act 250 – that requires landowners secure a permit from the Vermont Natural Resources Board before beginning activities such as commercial or industrial development, residential subdivisions, construction of communication towers, and mining or drilling (VTNRB 2008). If these activities are proposed within or adjacent to a known DWA, the Vermont Department of Conservation conducts an environmental review of the project to recommend strategies to avoid or mitigate impacts to deer habitat (J. Hazen, personal communication). The Vermont Fish and Wildlife Department may be consulted to assist with this review. About 3000 acres of DWAs are protected from development each year as the result of the review process required by Act 250 (S. Haskell, personal communication).

Maine's Land Use Regulation Commission

In 1971, the Maine Legislature established the Maine Land Use Regulation Commission (LURC 1997) to develop specific land use standards, create zoning boundaries, and guide development in Maine's 420 unorganized townships. LURC jurisdiction encompasses a total of 10.5 million acres, mostly in the northern 2/3 of Maine (C. Carroll, personal communication). Under its authority, LURC establishes Fish and Wildlife Protection subdistricts (P-FW); within these sub-districts, activities such as commercial timber harvesting and development are regulated to avoid jeopardizing significant wildlife habitat, including known DWAs (LURC 2007). The purpose of the P-FW subdistrict is to conserve important fish and wildlife habitats essential to the citizens of Maine because of their economic, recreational, aesthetic, educational, or scientific value (LURC 2007).

Only the shelter portion (dense conifer) of DWAs is protected by LURC zoning. To be protected, a DWA must be forested with >50% conifer stems, >50% conifer crown closure, and trees must average >10.5 m tall. Further, the DWA must support at least 20 deer/mi^2, although areas with fewer deer can be protected if LURC determines the area is needed to meet the purpose of the P-FW subdistrict (above). To de considered for zoning, MDIFW biologists must document deer use of the DWA in at least 2 of the past 10 years, and at least one of these surveys needs to be conducted on the ground; both surveys need to be conducted when snow conditions restrict deer to dense conifer cover (C. Hulsey, personal communication). LURC encourages landowners to work directly with biologists to determine what portions of their property will be zoned as a DWA. This is done by requiring biologists to either invite the landowner to accompany them during the ground survey, or at least meet with the landowner following the survey to discuss their findings and recommendations (C Carroll, personal communication). If the biologist and landowner can't agree on the specific area to be zoned, the landowner can appeal to LURC. In all cases, LURC makes the final determination on what area is zoned. Currently, 69,584 ha of DWAs are zoned as P-FW subdistricts (R. McKee, personal communication).

Once a LURC DWA has been zoned, landowners must comply with LURC standards for activities such as timber harvests and residential development within the zoned area. Non-motorized public recreation including hunting and fishing, motorized vehicle traffic on roads and trails, and snowmobiling are allowed within LURC-zoned DWAs without a permit (LURC 2007). Timber harvesting is allowed without a permit only if the landowner has a management or timber harvesting plan approved by a MDIFW biologist. MDIFW biologists are available to meet with landowners to conduct habitat assessments, discuss proposed timber harvesting plans, adjust plans to avoid impacts to and/or enhance DWAs, and to assist with harvest layout (C. Hulsey, personal communication). MDIFW has produced a set of management guidelines (Stadler 1987, MDIFW 1993) that serve as the basis for timber harvesting prescriptions in LURC-zoned DWAs (LURC 1997, L. Kantar, personal communication). If the landowner and biologists do not agree on a plan, or if the landowner doesn't have a plan, they must obtain a LURC-approved permit before they can harvest timber. Timber harvests cannot reduce the size of the zoned DWA to a level that will no longer meet the requirements of zoning.

Once a DWA is zoned as a P-FW, it cannot be removed from zoning unless it is documented that deer have not used the DWA for 10 years. LURC feels the standard for removing zoned DWAs should be strict because the purpose of the program is long-term habitat protection, but it recognizes that removal is appropriate in some cases (LURC 1997). If both the landowner and a MDIFW biologist agree that the DWA should be removed from zoning, it can be done without extensive documentation of no use (LURC 1997). In some cases, LURC will remove all or a portion of the zoning if a landowner can demonstrate that zoning creates a hardship greater than the benefit the public receives by having the area zoned (LURC 1997). In all cases, LURC has the final decision about what areas will be removed from zoning.

Is LURC-zoning effective in protecting DWAs in Maine?

The answer is complicated, but clearly LURC zoning could be more effective (C. Hulsey, personal communication; J. Pratte, personal communication; L. Kantar, personal communication; R. McKee, personal communication). One of the biggest limitations of LURC is that it only has jurisdiction within unorganized townships. DWAs within organized townships could be protected under the Natural Resources Protection Act which protects “significant wildlife habitat” (NRPA 2008). However, in order for individual DWAs to qualify as significant habitat, they must first be rated as high or moderate value to deer following a comprehensive ground survey (MDIFW 1993). Many DWAs in organized towns have been identified from aerial surveys, but budget constraints have not allowed MDIFW to conduct the ground surveys required to rank their value (C. Hulsey, personal communication). As a result, there is no specific protection afforded to DWAs in organized towns. Since they were initially identified in the 1990’s, >50% of the DWAs in organized towns have been lost due to liquidation timber harvesting, and in some towns all DWAs are gone (C. Hulsey, personal communication). To this end, DWAs zoned as P-FW by LURC are better protected than those within Maine’s organized townships which have no protection (C. Hulsey, personal communication; J. Pratte, personal communication; R. McKee, personal communication).

Within its jurisdiction, LURC's ability to protect a significant amount of DWAs is limited because it does not designate >3.5% of any WMD as P-FW subdistricts (LURC 2007). Private landowners challenged LURC zoning as a "land-taking" in the 1980s, but the Maine Supreme Court upheld the concept of zoning to protect wildlife populations, and DWA zoning in particular (LURC 1997). As a result, LURC considers its self-imposed 3.5% cap to be a compromise and the most appropriate way to balance competing uses of highly valued land within its jurisdiction (LURC 1997). If the 3.5% zoning cap is reached within a WMD, rezoning will focus on replacing lower priority DWAs with those of higher priority. However, few, if any WMDs have actually met the 3.5% cap because many DWAs don't meet the strict LURC criteria (C. Hulsey, personal communication). These criteria are probably the biggest shortcoming of LURC zoning for effectively protecting DWAs.

Following the legal challenges to LURC, there was clear need to identify DWAs in a manner that could be legally defended (C. Hulsey, personal communication). Because the size of a DWA expands and contracts year to year and within a winter due to differences in deer numbers and weather conditions, it is difficult to accurately delineate what constitutes the outer boundaries of a DWA. However, the critical shelter portion of a DWA is relatively easy to delineate when deep snow confines deer to dense conifer cover. As a result, the shelter of DWAs became the only portion to be delineated and protected by LURC zoning (C. Hulsey, personal communication; R. McKee, personal communication).

Some LURC-zoned DWAs have become non-functional

With few exceptions, landowners and biologists have been very successful in working together to develop timber harvesting agreements (Marston 1982, Willette 1982, R. McKee, personal communication). In general, landowners have followed the management plans approved by MDIFW and have adequately maintained the LURC-zoned portions of DWAs on their land (C. Hulsey, personal communication; J. Pratte, personal communication). However, in many cases, the areas outside of the protected zones are cut heavily (C. Hulsey, personal communication; J. Pratte, personal communication). So, although LURC-zoning is effective in protecting the area currently providing shelter, sustained growth of young softwood needed as future cover is compromised outside of the protected zone (J. Pratte, personal communication). In some cases, heavy timber harvesting outside of the LURC-zone is reducing the connectivity within DWAs and creating isolated islands of protected cover (J. Pratte, personal communication). This has resulted in many LURC-zoned DWAs becoming less functional (C. Hulsey, personal communication) as well as abandonment of some DWAs (J. Pratte, personal communication). Similar concerns have been raised on Crown Lands in New Brunswick where only the shelter portion of DWAs are specifically protected by regulations (Boer 1982, R. Cumberland, personal communication).

In general, LURC-zoning has been effective in protecting some DWA's, but the LURC-zoned area alone is not sufficient for maintaining the sustained health and function of a DWA (J. Pratte, personal communication), and it is not effective at protecting enough DWAs needed to support deer populations desired by the public (C. Hulsey, personal communication; L. Kantar, personal communication; R. McKee, personal communication). If land-use zoning is going to maintain functional DWAs into the future, the entire DWA must be protected, not just the portion that serves as shelter (C. Hulsey, personal communication; J. Pratte, personal communication). The challenge will be developing a program that can accurately identify a defendable outer boundary of a DWA, especially in Maine where the DWA needs of deer differ in southern and northern areas (Dickinson 1982). However, Maine landowners who voluntarily work with MDIFW to manage DWAs can avoid having their DWAs zoned by LURC. These "cooperative agreements" have had both positive and negative results in effectively maintaining DWAs on private land in the northeast.

Cooperative Agreements

A cooperative agreement is when a landowner, usually a commercial ownership, enters into an agreement with a public agency to voluntarily alter their normal timber harvesting practices in order to protect, or in some cases, manage DWAs on their land. The idea of cooperative agreements likely began in New Hampshire in the 1950's when Henry

Laramie, deer project leader at the time, developed the NH Deer Yard Management Project (Coulter 1982, Strong 1982, NHFG 1970). This program was supported by federal Pittman-Robertson funds and it involved soliciting voluntary cooperation from all of the commercial forestland owners in northern New Hampshire (Strong 1982). After 25 year of effort, this program resulted in 8000 ha of no-cut or postponed-cut prescriptions on private land and in the White Mountain National Forest which Strong (1982) described as “a very sizeable contribution to the public interest without any monetary compensation.” Since then Maine (Coulter 1982, C. Hulsey, personal communication), New Hampshire (K. Gustafson, personal communication), Vermont (S. Haskell, personal communication), and New York (Dickenson 1982) have used cooperative agreements as one tool for protecting or managing DWAs.

In most situations, cooperative agreements end up being operated as technical assistance programs where state wildlife biologists meet one-on-one with the forest manager to assess current DWA conditions, discuss forest management objectives, educate about DWAs and how they function, and develop and layout a cutting plan that will protect or enhance the DWA (NHFG 1970, C. Hulsey, personal communication; W. Staats, personal communication). There is generally compromise in the process to develop a plan that will benefit deer, but also allow the landowner to accomplish their primary objectives (C. Hulsey, personal communication; W. Staats, personal communication). In this process, biologists, forest managers, and landowners often develop long-term working relationships (J. Pratte, personal communication) that may continue despite change in landownership and timber harvest objectives (W. Staats, personal communication).

While cooperative agreements can work well, the fact that they are voluntary leaves a large amount of uncertainty concerning commitment and practice (NHFG 1970, C. Hulsey, personal communication; J. Pratte, personal communication; W. Staats, personal communication). Even if a forest manager and biologist agree upon a plan, ownership may alter or disregard it (J. Pratte, personal communication), or the land is sold and the process must begin anew (L. Kantar, personal communication). The success of cooperative agreements is ultimately determined by the landowner’s objectives and their willingness to manage their land for both deer and timber (W. Staats, personal communication). Both Maine and New Hampshire have maintained cooperative agreements with commercial landowners for >50 years by using regional biologists familiar with landowners and DWAs.

While cooperative agreements worked well in the past, recent changes in landownership have reduced their utility to perpetuate DWAs (C. Hulsey, personal communication; W. Staats, personal communication). In Maine, the 1990's represented a time when cooperative agreements were very successful (C. Hulsey, personal communication) because most commercial landowners managed their land for sustainable wood products (Hagen et al. 2005), they were concerned about their public image as stewards of the forest resource, and cooperative agreements had high public relations value or social capital (C. Hulsey, personal communication). However, new and current landowners such as Timber Investment Management Organizations, Real Estate Investment Trusts, and timber barons are often not interested in long-term management and may or may not practice sustainable forestry (Hagen et al. 2005, Fernholz et al. 2007). Ownership change and particularly change in management philosophy are major deterrents to voluntary cooperative efforts. Managing DWAs is a long-term proposition where landowners make current decisions based on 60+ year rotations; such long-term planning and investment is often incompatible with a management horizon of only 10-15 years (C. Hulsey, personal communication; W. Staats, personal communication).

Current cooperative agreements in Maine

Cooperative agreements offer some degree of flexibility in what proportion of a property is managed intensively for DWAs. Of the 5 signed agreements that the MDIFW currently has with commercial landowners, some pertain to an entire ownership, some to certain sections, and others to just specific DWAs (J. Pratte, personal communication). Landowners with signed agreements don't have to have their property zoned as a P-FW protection zone with LURC; however, most voluntary agreements require the landowner to adjust timber harvest objectives on more land than would be required if they were simply zoned by LURC (C. Hulsey, personal communication; J. Pratte, personal communication). These 5 agreements have worked well, but require the landowner to take extra steps in planning and meeting with biologists than would be required if they entered into LURC zoning (J. Pratte, personal communication). There is currently no obvious advantage or incentive for landowners to voluntarily agree to adapt their timber harvests to maintain DWAs on their land.

Property tax incentives

One potential option for encouraging landowners to voluntarily manage DWAs is to offer property tax incentives. Vermont, New Hampshire, and Maine all have some form of current land use tax appraisal that compensates landowners who actively manage natural resources such as timber and wildlife habitat. These programs recognize that there are costs associated with management such as hiring consulting foresters, improving forest access, and creating management plans (SPACE. 2008). Managing DWAs requires these and additional costs associated with delaying timber harvests and/or reducing the volume of timber harvests. As early as 1981 (and probably much earlier) landowners asked whether those with LURC-zoned deer yards could be compensated with reduced property taxes (Bessey 1982). If public demand for deer resources results in a significant monetary loss to private landowners, perhaps it is warranted to provide some level of property tax relief to those who demonstrate a commitment to conserving and perpetuating DWAs. Maine's Tree Growth Tax Law (DCMFS 2008b) and New Hampshire's Current Use - Forest Land with Documented Stewardship (SPACE 2008) programs provide the initial framework for how such a tax program might be structured.

Financial incentives

Few states provide financial incentives to landowners specifically to reimburse them for managing deer habitat. The New Hampshire Fish and Game Department has a Small Grants Program that is funded through a fee assessed on hunting licenses. This money is used to fund a variety of general habitat improvement projects, and those conducted specifically to benefit deer include release of softwoods in historic DWAs, cool/warm-season forage plantings, release of mast trees, and fruit and shrub planting. In Minnesota, funds are available to reimburse landowners who plant conifers for deer winter cover (R. Horton, personal communication).

Considering the high value of spruce-fir sawtimber, it probably isn't possible or practical to directly compensate landowners for not cutting wood (W. Staats, personal communication). However, other activities associated with managing DWAs, such as developing written management plans and mapping and monitoring DWAs are a direct cost to a landowner that could be reimbursed partially or fully. Funds from the New Hampshire Small Grant Program have been used to compensate landowners who developed wildlife habitat management plans. Reimbursements might provide a small incentive for landowners who enter into voluntary cooperative agreements to manage DWAs. The obvious challenge to this approach is establishing a source of funding to support a meaningful and effective incentive program.

Land Leases

In 1956, the New Hampshire Fish and Game Department decided that in order to save an important DWA, the best approach was to lease half of it in order to manage it effectively to benefit deer (Strong 1982). Currently, no states lease land for the purpose of managing DWAs. However, this may be a reasonable option for a specific DWA identified as critical to meet local deer population goals. Again, the obvious limitation to this option is identifying a source of funding.

Conservation easements

State agencies in Michigan, Vermont, New Hampshire, and Maine either directly hold conservation easements on properties with DWAs or participate in the management of DWAs on properties protected by conservation easements held by other agencies or organizations (B. Scullon, personal communication; J. Pratte, personal communication; S. Haskell, personal communication; W. Staats, personal communication). For example, MDIFW has a biologist on staff hired to oversee management of DWAs on easements held by the Maine Bureau of Parks and Lands (J. Pratte, personal communication). Most conservation easements provide permanent protection from future development. Further, many specify types of activities allowed on the property (e.g., timber harvesting), along with standards associated with those activities (e.g., an agency-approved management plan). A primary benefit of conservation easements is that they provide insurance that investments to improve wildlife habitat won't be lost as the result of development of the property. Further, most easements are held by at least two holders (e.g., a state wildlife agency and non-profit organization) who are responsible for ensuring that any activity on the property is conducted following the standards or restrictions specified in the easement.

Considering that DWAs in most states represent a relatively small proportion of the land area (e.g., 3% in NH and 4% in Maine), conservation easements may be a viable option for protecting and perpetuating DWAs into the future (W. Staats, personal communication). Easements will be most suitable for properties that contain DWAs that are identified as critical for meeting deer population goals. Focus should probably be given to properties that contain all or a significant proportion of a DWA to ensure that its function is maintained long-term. Boer (1992) suggested that because DWAs >100 ha are more stable and less likely to be abandoned; they should be given priority over smaller DWAs. While DWAs that provide functional winter shelter to deer are obvious candidates for protection, in some cases it might be beneficial to protect areas that will develop into a functional DWA. Probably the biggest drawback of conservation easements is finding a source of funding to secure the initial easement, as well as additional funds needed to manage until timber harvests can help offset management costs.

Outright purchase

Although direct land purchase is the most expensive option to protect DWAs, this option provides permanent control in their management. In 2002, Michigan DNR developed the Winter Deer Habitat Conservation Initiative funded solely by a $1.50 fee on hunting licenses; this program raises $2.5-3 million annually to fund the purchase and management of land with high priority DWAs (B. Scullon, personal communication). In the past six years Michigan DNR has secured an additional $11 million from the

Michigan Natural Resources Fund, a fund supported by revenue generated from oil and gas leases on state land. Funds from these two programs were used to purchase 5,200 ha of high priority DWAs, mostly in the Upper Peninsula. Michigan DNR also partners with other organizations to purchase land. Despite the expense, Michigan DNR and the public recognize that DWAs are critical to maintain deer and support efforts to secure and manage properties containing high priority DWAs (B. Scullon, personal communication).

Mapping and monitoring DWAs

While many states conducted extensive efforts to map and inventory DWAs in the 1970-1990s (e.g., ME, NH, VT, NY), little effort to monitor those DWAs or to identify others occurred due to budget constraints, limited personnel, and other agency priorities (C. Hulsey, personal communication; J. Hurst, personal communication; S. Haskell, personal communication; W. Staats, personal communication). The utility of DWA maps declines when deer activity and use are not monitored annually within DWAs (Boer 1992). The impact of agencies not conducting this work is evident in the substantial loss of DWAs in the organized townships of Maine (see above). Any of the above efforts to zone, conserve, manage, or create functioning DWAs will only be successful if agencies are able to collect and maintain accurate information about DWAs. Efforts to secure funding for protection and management programs should include support for inventory to best promote sustainability of DWAs.

CHAPTER IV: ISSUES IN HUMAN DIMENSIONS

Management of deer populations and DWAs on commercial forestland presents a unique situation of balancing a valuable, high-profile public resource (deer) that is critically dependent upon privately-owned, specialized forest habitat with high economic value. Binding public referendums in Maine regarding recent forest-wildlife issues (i.e., moose hunting in 1983, forest management practices in 1997, bear baiting in 2004) demonstrate the measurable and increasing concern, value, and influence of stakeholders in natural resource management conflicts. Stakeholders associated with management of DWA in Maine include industrial and private landowners, MDIFW, investment groups, outdoor recreationists, hunters, conservation groups, residents, tourists, and more.

Unfortunately, stakeholders often bring strong societal, political, and economic influence to an issue while having highly varied knowledge, sense of cooperation, and economic concerns. Their voices, values, and uses include recreation, use and exploitation of resources, economics, access, populations, scenery, esthetics, and resource and ecosystem health. Regulatory power obviously influences management of deer populations and to some extent DWA. However, few suggest or believe that political regulation of forest management practices offers the best approach to long-term cooperation among stakeholders, as well as management and sustainability of Maine's working forest, and deer and DWA management. Given the recent high profile use of forest-wildlife referendums or "ballot-box biology" in Maine, implementation of a more effective human dimensions approach to forest-wildlife management may be beneficial.

A human dimensions approach in wildlife management essentially acknowledges that a human-wildlife conflict or issue exists, and that the issue involves stakeholders with varied values and expectations. The solution is about the process as much as the end-result, and necessarily involves stakeholder involvement and voice (Decker and Chase 1997). Participation in the process is the primary value to stakeholders, not simply input (Stout et al. 1996). Wildlife management by state agencies was traditionally the "expert" (agency dominated) approach, but increasingly, human-wildlife issues have forced a gradual shift to more stakeholder involvement both by practice and demand. Regionally, many deer management issues in New York State have been addressed with human dimensions where stakeholder involvement has progressed to a co-managerial (agency partnerships with stakeholders) approach in certain situations; however, no one approach fits all issues, or guarantees a permanent solution (Chase et al. 2000).

The use of a human dimensions approach raises potential problems and concerns for public agencies responsible for managing wildlife, including shared responsibility, releasing "ownership", and question of authority. However, legal authority is clearly stated in federal and state legislation, and improved support from better educated and involved stakeholders should provide long-term benefit both politically and economically (Chase et al. 2000). Successful stakeholder involvement requires that scientific information be used and accepted, stakeholders are treated fairly and have some influence in decision-making, and communication and education are promoted (Chase et al. 2002). The concept of acceptance capacity can be used to evaluate the range of outcomes or solutions to an issue, and is directly related to the varied impact perceptions of stakeholder groups (Lischka et al. 2007). Because most human-wildlife issues are not solved permanently, linking adaptive resource management (better science) and adaptive impact management (better integration of ecology and human dimensions) should promote adaptive wildlife management (Enck et al. 2006). Adopting an effective human dimensions approach seems ideal given the complexity of the human dimensions of managing deer populations and DWAs.

Management of most DWAs in New England was accomplished traditionally without regulatory protection, rather, it occurred via landowner-agency agreements where both parties recognized the ecological and economic value of a DWA. Ironically, such traditional agreements probably represent some of the best co-managerial examples of wildlife management, long before human dimensions, shareholders, and such became in vogue! Thus, most landowners had what is termed social capital, or value of community engagement and responsibility for mutual benefit that requires and brings trust and reciprocity. Interestingly, social capital increased with ownership longevity and declined with absentee ownership in deer associations in Texas (Wagner et al. 2006). This direct relationship between ownership longevity and social capital raises concern in Maine because of the rapidly changing ownership patterns of Maine's commercial forests. About 1/3 of Maine's forest has changed hands since 1998, and traditional ownership (forest industry) has declined from 60 to 15%, while investment groups now own about 1/3 of Maine's commercial forest (Hagan et al. 2005).

Ownership patterns will obviously affect the long-term management strategies and sustainability of Maine's commercial forests. New ownerships in Maine include five primary types: two investment groups including TIMOs (Timberland Investment Management Organization) and REITs (Real Estate Investment Trust), timber barons, private individuals, and non-profit conservation groups (Hagan et al. 2005). Ownership longevity of investment groups is about 10-15 years (Fernholz et al. 2007), suggesting that investment groups might be akin to absentee ownerships. Although investment groups clearly own timberlands for economic return, most harvest in a sustainable manner unlike many new contractors and timber barons (Hagan et al. 2005). The very nature of their investment has both positive and negative aspects; security and stability in land appreciation and value encourage investment, but eventual subdivision and development eventually provide higher return (Fernholz et al. 2007). Although the contiguous commercial forest has largely remained intact, it is characterized by more varied and smaller ownerships (Hagan et al. 2005); continual selling and subdivision of commercial forests will make their sustainability harder (Fernholz et al. 2007). However, non-profits are often able to work with investment groups to secure conservation easements under SFI guidelines (Fernholz et al. 2007), indicating that social capital is not absent from new landowners.

A human dimensions approach in DWA management provides an ideal opportunity to further develop valuable social capital and acceptance capacity for new commercial forest ownerships in Maine. Surveys of Maine residents (Sargent-Michaud and Boyle 2002) and residents of the Great Northern Forest (NY, VT, NH, ME; Enck and Brown 2006) indicate that the public has poor understanding of forest-wildlife ecology and management, but have opinions about forest management activity (as also evidenced in

Maine's 1997 referendum). Surprisingly, about half had a positive attitude toward both mature and early successional forest stages, but low satisfaction about agency activities, and tended to focus on personal, identifiable benefits from the forest. Residents have both anti-management and utilitarian values; in total, the survey data indicated disconnect in many efforts to engage and educate the public.

Thus, linking very specific desirable outcomes and benefits (e.g., deer and DWA management) to forest harvesting practices presents an opportunity to affect and improve societal attitudes and support for practical forest management. For example, deer have been used in Texas to promote social capital within associations and to encourage further cooperation in management of other resources (Wagner et al. 2006). In turn, both management-regulatory agencies and forest ownerships should gain social capital and acceptance capacity. Promoting socially responsible investment, forest certification and SFI, and cooperative agreements with a reward system based on currency (e.g., tax credits, habitat credits) should further advance social capital of forest ownerships (Hagan et al. 2005, Fernholz et al. 2007). Key to this process, however, will be a truly open human dimensions approach; because the relative knowledge of the public is low, there is tremendous opportunity to educate many stakeholders to ensure that decisions, policy, and agreements are based on the best science not opinion.

Permanent solutions are unlikely in dynamic forest-wildlife management issues largely affected by weather and habitat such as deer and DWA management. Probably as consequential to the issue, is the rapidly changing land ownership (Hagan et al. 2005) and investment patterns in Maine forestland (Fernholz et al. 2007), and the potential regulatory power of Maine citizenry through the public referendum process. A human-dimensions approach should reveal that a number of opportunities and strategies exist to more effectively manage deer and DWAs on Maine's commercial forestland to benefit both the resource and forest ownerships. Given the myriad of stakeholders, high social status and value of deer, the low-moderate public satisfaction with state agencies, and the dynamic status of forest ownership, a key decision will be identifying a group capable of implementing and maintaining an objective approach.

CHAPTER V: SUMMARY AND RECOMMENDATIONS

Winter Ecology of Deer

1) The northern range of white-tailed deer is presumably limited by snow depths that inhibit mobility and access to forage beyond their ability to withstand a negative energy balance in winter. All deer occupying a deer wintering area (DWA) will experience a negative energy balance or weight loss in winter (assuming they have no access to supplemental food).

2) The primary function of a DWA is to ameliorate severe winter conditions that increase exposure and energy expenditure of deer, inhibit their mobility, and reduce forage availability compared to other forest stands that provide less canopy cover.

3) All winter forage of deer is of moderate-low quality from a nutritional standpoint. Therefore, forage availability and intake are of most importance from the standpoint of energy balance, not specific forage species. Nutritional value and intake rate tend to decline throughout winter as deer remove the current annual growth (CAG) of most browse, and increasing snow depth reduces access to forage. Because intake rate is directly related to the digestibility of the diet, providing high forage diversity and availability should help maintain higher intake rates.

4) The seasonal fat cycle in adult does is their primary adaptation to withstand extended periods of limited forage availability in winter. Adult does typically have body fat >20% in early winter; conversely, fawns have 15% or less. Body fat accounts for 35-50% and 10-25% of the daily energy expenditure (DEE) of adult does and fawns, respectively, during a 90-100 day period of confinement in a DWA. The reciprocal amounts are met by forage consumption; any reduction in forage consumption would increase the contribution of fat to the DEE. Therefore, on a relative scale, survival of adult does is most influenced by length of winter, whereas survival of fawns is most dependent upon constant forage intake.

5) Measurements of DEE and energy balance models indicate that energy conservation is the primary survival strategy of deer to limit their negative energy balance in winter; the average DEE of deer is considered low and similar to their maintenance energy requirements (1.6-1.8 x FMR). Therefore, energy cost of thermoregulation and activity/travel are minimal for deer in winter, as also indicated by laboratory measurements and their behavior associated with mobility and travel in DWAs.

6) Measurements of DEE and energy balance models indicate that deer mortality should be expected when severe winter conditions extend beyond 90-100 days. Fawns experience earlier and higher mortality than adult deer because, on a relative basis, they have higher fasted metabolic rate (FMR), less body fat, higher DEE, and less access to forage due to their age and size.

7) Measurements of DEE and energy balance models indicate that enhancing metabolizable energy intake (MEI) is the best strategy to increase survival of fawns and productivity of adult does. Therefore, maximizing browse availability and enhancing mobility to improve access to browse should be promoted in DWA management.

8) The most influential factor of winter survival of deer in DWAs is forage competition that is a function of high population density in a confined area with limited resources. Snow depth primarily influences forage availability and mobility of deer within a DWA and largely dictates forage competition and malnutrition. Therefore, managing for high forage availability is key to promote survival and reduce mortality in a DWA.

9) Coyotes are the major predator of white-tailed deer during winter when deer are confined in DWAs. The predatory interaction of deer and coyotes is analogous to that of deer and wolves; sustainability of local coyote populations in northern forests is probably a function of deer predation because alternative prey for coyotes is limited in winter.

10) Coyote predation is influenced mostly by winter severity that restricts mobility of deer, and their abundance, distribution, and relative vulnerability. Coyotes predate all sex/age classes of deer but fawns are most vulnerable. The vulnerability to predation is greatest in low density populations in small DWAs; large DWAs with higher density of deer may have reduced predation rates because of better habitat conditions.

11) Predation is greatest when forage competition and malnutrition occur in late winter. Thus, the probability of additive mortality from predation is influenced by winter conditions that exacerbate all mortality factors, as well as the physical characteristics of a DWA that influence condition of deer. Thus, management of DWAs should focus on maintaining high browse availability and mobility of deer.

12) Predation by coyotes has been implicated in many local and regional declines of deer populations. Well-established coyote populations in Maine should be considered a permanent source of winter mortality that has effectively lowered the carrying capacity for deer where deer are confined to DWAs for extended periods. Historic population goals established during periods of coyote-free DWAs are likely not attainable. Deer population goals need to reflect coyote predation during winter.

13) Coyote predation should be considered a limiting not regulatory factor of deer populations (assuming lower carrying capacity). Depressed regional deer populations in Quebec have recovered after a series of mild winters, habitat restoration, and coyote population control. Maintaining DWAs with optimal forage and mobility that enhance body condition and lower vulnerability of deer should reduce the relative amount and impact of coyote predation.

14) Deer typically have reduced productivity after severe winters because of high mortality and reduced body condition of does that affects fecundity and fawn survival. The impact of a severe winter could be measured for 2-3 years, but should be considered a lagged, not cumulative effect. A series of consecutive severe winters that continually depress productivity can produce regional population declines.

15) A series of mild winters is probably required to grow a depressed deer population at its northern extent. Mild winters reduce mortality from malnutrition and predation, and promote higher productivity through improved nutritional status and body condition of yearling and adult does. The impact of severe winters on northern deer populations is best addressed by maintaining large DWAs that provide optimal cover, forage, and deer density.

16) DWAs generally represent only 5-15% of the area that deer use throughout the year; deer in the northeast may travel >30 km to occupy a DWA. Therefore, factors that affect the survival and productivity of deer in a local DWA can influence deer over a wide geographic range. It is important for managers to know the source of deer in large DWAs.

17) Deer display very strong fidelity to their DWA and are very reluctant to abandon it. This has several implications to DWA management including 1) habitat improvement should focus on DWAs currently used by deer, 2) colonization of a DWA where deer are removed (e.g., predation, severe winter) will probably not be immediate, 3) what happens to deer when their DWA is removed is unknown. A study designed to investigate 2) and 3) is warranted.

Ecology and Management of Deer Wintering Areas

18) All DWAs are comprised of two basic habitat components; mature conifer stands that provide deer shelter and improve their mobility, and other forest or non-forest habitats that provide forage. The best DWAs contain high interspersion of cover and food that provide deer access to resources throughout winter under a wide range of snow conditions.

19) Snow depth, usually $\geq$30 cm, is the main factor that triggers deer to occupy DWAs; deer become confined to dense conifer stands when snow depth exceeds 40-50 cm. The use of a DWA expands and contracts constantly as snow and sinking depth influence deer mobility.

20) When snow is deep, mature conifer stands with dense canopy cover provide deer with the best access to browse and alternate foods such as lichens and litterfall. Hemlock and northern white cedar are considered superior to other conifers in providing winter cover for deer and should be retained within DWAs whenever possible. Balsam fir and spruce are moderate in their cover value and require somewhat denser stands to intercept snow.

21) The best winter cover for deer is provided by mature forest stands that are comprised of at least 50% conifers with 50% crown closure, and at least 10 m tall. Exactly how much conifer cover deer require is unknown. In areas where snow depths regularly exceed 50 cm, deer may require conifer stands with at least 70% crown closure. In areas where snow depths rarely exceed 20 cm, 30% conifer cover may be adequate.

22) It unknown exactly how small a conifer stand can be and still provide functional cover for deer. However, DWAs >100 ha should be the focus of management and conservation efforts. Larger areas are more conducive to managing cover and browse under a shifting mosaic that should benefit both deer and timber management. It is unknown how deer colonize new DWAs in a landscape has been heavily fragmented by timber harvesting, and study of such is warranted.

23) Extensive commercial clear-cutting that removes softwood and creates abundant browse reduces the carrying capacity of deer winter habitat in northern Maine. Timber harvesting that maintains or enhances the interspersion of functional conifer cover and abundant browse is most likely to benefit deer.

24) Three main objectives should be considered when creating and maintaining an ideal DWA including:

1) Maintain an adequate amount of functional cover at all times,
2) perpetuate a constant, abundant supply of accessible forage, and
3) maintain a high level of interspersion and mobility that provides functional cover and accessible food.

25) Best Management Practices for managing DWAs should be developed to provide foresters, loggers, and biologists with practical methods for accomplishing the three objectives in #22 for creating ideal DWAs on lands managed for commercial timber.

26) DWAs should be managed using “area regulation” to ensure that at least 50% of the DWA provides functional conifer cover at all times. Silviculture in DWAs should promote a variety of age-classes; stands should not become over-mature and harvesting strategy should promote a series of "on-line" conifer stands to replace those that are harvested.

27) Silvicultural techniques to manage spruce-fir timber can be identical to those used to create ideal DWA conditions. How these techniques are applied to accomplish both goals on the same property will require creativity and compromise on the part of both the landowner and any regulatory agency.

28) Uneven-aged silviculture, and especially group-selection, is preferred over even-aged silviculture for managing the cover component of DWAs. Group-selection retains the densest pockets of conifer cover while allowing hardwood browse and new conifers to regenerate.

29) When uneven-aged silviculture is not an option, even-aged silviculture should be used to maintain a diversity of age-classes across the DWA; while individual stands are even-aged, the overall DWA will be uneven-aged to ensure that a constant supply of functional cover is maintained while timber is harvested.

30) Thinning can be used to develop young conifer stands into functional cover at a younger age and lengthen the amount of time a stand can provide functional cover for deer.

31) Optimum browse production can be maintained by managing browse areas on a 40 year rotation where 25% of the area is regenerated every 10 years. At least some browse cutting should be conducted every 10 years to ensure there is a constant supply of accessible browse.

32) Linking snow depth and time of confinement to a DWA has long been advocated as a reliable measure of winter severity. A winter severity index (WSI) reflects the direct relationship between winter severity and the body condition, productivity, and mortality of wintering deer, and is probably the most useful tool that deer managers have to adapt and adjust annual harvest goals to address long-term deer population goals. A typical WSI uses a combination of measurements of snow depth, sinking depth, and ambient temperature - calculated as total "days" or points - to produce severity scores with thresholds that predict relative winter severity and mortality.

33) The use of a WSI offers many advantages including annual assessments and management responses, as well as long-term data sets. These data are valuable for analyses of weather and herd response, temporal evaluation of a DWA as it ages or is harvested, and to compare biological and economic value of a DWA.

34) A long-term evaluation of the number of days with 50 cm snow depth could be useful to produce a stratified, geographical approach in managing DWAs. Maine could be divided into three habitat management zones based on differences in average winter severity. These zones could be used to establish criteria for minimum crown closure in each zone (e.g., 70% in north, 50% in central, 30% in south).

Human Dimensions and Management

35) The primary human dimensions issue in managing highly valued deer in Maine is maintaining and managing DWAs on commercial forestlands. Forest-wildlife issues in Maine have a recent history of contentious public referendums that demonstrate highly varied stakeholder groups with wide-ranging values, knowledge, and economic and political influence.

36) The recent proliferation of large forestland ownerships by investment groups (e.g., REIT and TIMO) in Maine, and their tendency for short-term forestland ownerships (10-15 years) has raised concern about long-term forest-wildlife management issues, specifically, the availability and sustainability of DWAs.

37) Voluntary cooperative agreements have been used as a viable option for maintaining functional DWAs on commercial forestland. However, recent changes in land ownership are reducing the viability of cooperative agreements as an effective conservation and management tool. There are few incentives that encourage landowners to enter voluntary agreements and accept restrictions on their property. These changes have led, in part, to land use zoning and related timber harvest regulations to manage DWAs.

38) In unorganized townships in Maine, land use zoning through the Land Use Regulation Commission (LURC) restricts timber harvesting in an effort to manage and protect DWAs. However, LURC zoning is insufficient for maintaining functional DWAs long-term because it only protects the shelter portion of a DWA. LURC zoning would be more effective if it regulated timber harvesting in a larger portion of a DWA to manage other resources important to deer.

39) LURC might consider establishing some form of "hold harmless" clause for landowners cooperating in DWA management. Limiting the area of potential zoning could be an incentive to encourage landowners to enter voluntary agreements to help maintain and manage DWAs on their property. Where landowners are required to manage DWAs cooperatively with MDIFW or through LURC zoning, recognizing the lower proportion of conifer cover needed by deer in central and southern Maine (see #41) may improve landowner cooperation.

40) The concept of social capital will likely be important in encouraging landowner cooperation and appreciation of long-term management of DWAs. Ironically, traditional cooperative agreements for DWA management were, in large part, a function of social capital because industrial forest owners were vested in local natural resource issues by default. Such agreements were also representative of a co-managerial approach to DWA management, an approach advocated in complex wildlife management issues.

41) Conservation easements can be effective in restricting development and specific timber harvesting practices that result in negative impacts to DWAs. Considering that DWAs comprise such a small part of Maine's land base, it may be appropriate to direct public funds toward securing easements on DWAs that are critical to meet regional deer population goals. Further, if public demand for deer resources results in a significant monetary loss to private landowners, it may be warranted to provide some level of property tax relief to landowners who demonstrate a commitment to conserving and perpetuating DWAs.

42) It may be justified to allow landowners to make larger clearcuts on properties where cooperative agreements with MDIFW are in place to manage DWAs. Restricting the area that can be clear-cut under the Maine Forest Practices Act may actually reduce landowner flexibility in managing timber harvests. Specifically, restricting clear-cut size forces landowners to spread their harvesting across a greater portion of their property and may reduce their flexibility in setting areas aside to be managed as DWAs.

43) Identifying, zoning, managing, and conserving DWAs requires accurate and current knowledge about where DWAs occur and to what extent they are used by deer. This information can only be collected through organized efforts to map and monitor DWAs continuously. If deer are identified by the public as a priority, public funds should be devoted to a program that will allow regular mapping and monitoring of DWAs.

44) The traditional "expert" or authoritative approach of management is not recommended to address the DWA issue in Maine, rather, a co-managerial approach that will require shared responsibility is advocated. Given the myriad of stakeholders and their varied knowledge and attitudes, high public value and sentiment for deer, dramatic shifts in land ownerships and turnover, economic issues, and recent history of public referendums, strong and responsible leadership by one organization is needed to implement an objective and successful human dimensions approach to address deer and DWA management in Maine.

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