

Effects of Snow on Sitka Black-Tailed Deer Browse Availability and Nutritional Carrying Capacity in Southeastern Alaska

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ABSTRACT Snow affects the nutritional ecology of northern ungulates during winter through burial of important winter forages. We used nonlinear regression analyses to model snow-burial dynamics of blueberry (*Vaccinium* spp.) browse biomass, a key winter food item of Sitka black-tailed deer (*Odocoileus hemionus sitchensis*) in southeastern Alaska, USA. During November 2003–March 2004 we collected data from 546 individually marked twigs located on 100 plants of differing sizes and architectures across a range of snow depths. In general, browse biomass became buried and unavailable to deer at snow depths substantially lower than prewinter twig heights. Plant architecture and plant height were related to the probability of a twig being buried. Probability of twig burial was higher on plants with lateral than on those with erect architectures. Twig height also affected the probability of burial by snow but the relationship was complex. For twigs located on erect plants, probability of burial was greatest for twigs near the bottom and top of the plant due to ground-up burial and bending of flexible apex stems, respectively. We used estimated nonlinear equations to model blueberry browse availability in a simulated upland old-growth habitat patch subject to a range of snow depths. We then compared subsequent estimates of deer winter nutritional carrying capacity for this habitat patch to findings derived using an alternative, simple linear (ground-up) model of winter-browse burial by snow. Comparisons indicated that ground-up models of browse burial overestimated browse availability and nutritional carrying capacity for most snow depths. Our findings demonstrate the importance of applying detailed snow-burial models when characterizing nutritional landscape of northern ungulates during winter. (JOURNAL OF WILDLIFE MANAGEMENT 73(4):481–487; 2009)

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Sitka black-tailed deer (*Odocoileus hemionus sitchensis*) are an important species both ecologically and culturally in temperate forest ecosystems of North America (Hanley 1993). Environmental variability, particularly during winter, influences many aspects of deer ecology, especially in populations near distributional extremes. Southeastern Alaska is the northern-most extent of native Sitka black-tailed deer range and populations in this region are strongly influenced by factors associated with winter severity, such as snow depth and persistence (Klein 1965, Wallmo 1981). Previous studies have documented strong behavioral responses of deer to winter snow accumulation. Specifically, seasonal habitat shifts from high to low elevations and from open- to closed-canopy habitats at lower elevations in response to increasing snow accumulation have been observed (Schoen and Kirchhoff 1985, 1990). Such habitat shifts are likely driven by high energetic costs associated with locomotion through snow (i.e., Parker et al. 1984) as well as increased snow burial of preferred winter forages in more snowy, open habitats (Kirchhoff and Schoen 1987). Consequently, snow accumulation can have important implications for deer nutritional ecology and energetics during winter (Parker et al. 1999) and ultimately influence reproductive success, survival, and population dynamics.

In southeastern Alaska, USA, effects of snow on the winter energy budget of black-tailed deer are much greater

in reducing energy intake (via burial of forage) than in elevating energy expenditure (via increased cost of locomotion; Hanley and McKendrick 1985, Parker et al. 1999). Winter diets of deer are primarily composed of evergreen forbs, shrubs, and conifers, in order of decreasing preference and nutritional quality (Hanley and McKendrick 1985). Because evergreen forbs, the most nutritious winter food items, are often buried by snow, deer forage extensively on shrubs and, to a lesser extent, conifers during snowy periods or during moderate–severe winters. Consequently, even though winter diets lacking evergreen forbs are of much lower nutritional quality than forb-dominated diets (Hanley and McKendrick 1985), availability of shrub forage biomass plays an important role in regulating loss of deer body condition during winter when deer are experiencing a negative energy balance (Parker et al. 1999). As a result, determining how snow accumulation influences availability of shrub forage biomass is important for understanding the nutritional and energetic landscape that deer encounter during snowy winter months.

Blueberry (*Vaccinium* spp.) is the most abundant and heavily utilized shrub species found in black-tailed deer diets in old-growth forest wintering habitats. However, the relationship between snow accumulation and the availability of blueberry forage biomass in northern coastal ecosystems is not well understood. Previous studies in more southerly and interior climates documented that burial of browse under snow is best described by nonlinear functions related to

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snow depth and prewinter height of browse biomass (Jenkins et al. 1990, Hovey and Harestad 1992). However, little is known about whether such relationships accurately predict shrub burial patterns in northern coastal environments that are characterized by snow accumulation and ablation patterns different from those in more southerly or interior locations. In addition, plant architecture (i.e., whether plants exhibit lateral or erect growth forms) likely plays an important role in determining whether plants deflect or accumulate snow. Yet, the way plant architecture influences probability of burial has not been previously explored.

The relationship between snow depth and browse availability for deer has been characterized as a linear ground-up function. In this framework, twig biomass at a set prewinter height is assumed to be available to foraging deer until snow depth reaches the set height and snow burial occurs (i.e., slope = 1). Although ground-up models may accurately describe winter shrub biomass availability in some circumstances (Hobbs 1989, Visscher et al. 2006), limitations exist depending on the forage-plant community composition and environmental conditions. When key forage plants are composed of highly flexible stems or evergreen leaves, accumulation of snow on plant surfaces may result in plant bending and premature burial (Jenkins et al. 1990, Hovey and Harestad 1992). Under such conditions, ground-up snow-burial models provide misleading estimates of winter forage availability and more detailed nonlinear models may be more appropriate (Jenkins et al. 1990).

Our objective was to examine how snow influences winter habitat ecology of black-tailed deer by focusing on factors that affect snow-burial dynamics of a key winter-browse species. Specifically, we investigated 1) how plant architecture, prewinter-browse height, and snow depth influence availability of blueberry browse biomass for deer during winter, and 2) how these factors ultimately affect the nutritional carrying capacity of deer.

STUDY AREA

We collected data during November 2003–March 2004 in a 41-km² study area located in the Fish Creek watershed on Douglas Island, near Juneau, Alaska (58.3°N, 135.5°W). We confined sampling efforts within the watershed to areas below 450 m, the principal wintering areas for deer in this region. Vegetation in the study area was typical of coastal northern temperate forest ecosystems and was composed primarily of a mosaic old-growth Sitka spruce (*Picea sitchensis*)–western hemlock (*Tsuga heterophylla*) and poorly drained mixed-conifer muskeg forest types. Woody shrubs including blueberry (*Vaccinium alaskaense*, *V. ovalifolium*, *V. parvifolium*) and false azalea (*Menziesia ferruginea*) were widespread and dominated the forest understory. Climate was characterized by cool, wet summers and snowy winters, although rainfall and freeze–thaw events occurred periodically throughout winter at elevations up to 800 m. In Juneau, snowfall occurred at sea level from November to

April and long-term (1943–2006) average temperature and snowfall at sea level for this 6-month period were -0.4° C and 240 cm, respectively.

METHODS

During September 2003, we established 4 0.25-km² study sites along an elevation gradient ranging from 200 m to 660 m that roughly bisected the center of our study area. At each study site we selected 25 blueberry plants at random along wandering transects (random distance and angle between plants). We did not distinguish between species of blueberry plants because morphological characteristics expected to affect snow burial are very similar among these 3 species. For each plant, we measured rooted stem diameter (mm) and height (cm). We also determined whether each plant had a lateral or erect growing posture, as determined by the angle of the plant stem axis ($<45^{\circ}$ = lateral, $>45^{\circ}$ = erect). Additionally, for each plant we systematically marked individual current annual growth twigs with small, neon orange, aluminum tags (1.5 cm², 0.07 g). We attached one twig tag for approximately each 1 g of twig biomass per plant (marked twigs/plant, \bar{x} = 6.28, range = 3–20). We subsequently measured perpendicular height (cm) of the marked twig to the snow-free ground surface (hereafter prewinter ht). We placed permanent snow-measuring stakes, graduated at 1-cm intervals, within 0.5 m of the base of each plant.

Beginning with the first winter snowfall, we conducted monitoring surveys at 7–10-day intervals. During each survey, we visited every plant to measure snow depth and determine whether individual marked twigs were buried under snow. At the end of the winter sampling period, we conducted a final survey to determine if all aluminum tags were still attached to each twig. If a tag was no longer attached, or otherwise accounted for, we removed data associated with that tag from the data set. Censoring these data was necessary to reduce the likelihood of falsely concluding twigs with lost tags were buried when they might not have been.

To evaluate factors related to whether a tag (hereafter a twig) was buried by snow, we used generalized mixed linear models (binomial errors and logit link; Littell et al. 2006), which also is referred to as logistic regression with correlated errors (Hosmer and Lemeshow 2000). We determined the response variable, whether the marked twig was buried by snow, for each of the 11 sample occasions during winter. The fixed predictors we considered in the models were snow depth, twig height, maximum plant height, basal diameter, and plant architecture. To account for the repeated measurements on individual plants and twigs on a plant, we included individual plants and twigs within plants as random effects under the assumption that responses of twigs on the same plant were likely to be more similar than responses of twigs on different plants and that, within a plant, repeated responses for the same twig were more likely to be similar than responses of other twigs. We also considered a model that allowed for temporal autocorrela-

Table 1. Statistical summary of blueberry-twig prewinter height-profiles for each plant-height quartile group used to produce snow-burial probability curves. We collected data during November 2003, Fish Creek, Alaska, USA.

Architecture	Plant ht (cm)			
	≤72	73–94	95–124	>124
Erect				
Min.	13.0	25.0	33.0	35.0
25%	32.0	50.0	70.0	86.0
Median	40.0	60.0	89.0	104.5
75%	49.0	69.0	100.0	123.0
Max.	65.0	90.0	116.0	152.0
<i>n</i>	79	91	123	78
Lateral				
Min.	11.0	30.0	47.0	24.0
25%	30.0	51.5	58.5	68.0
Median	38.0	62.5	77.5	94.0
75%	44.0	68.0	87.0	117.0
Max.	66.0	89.0	90.0	174.0
<i>n</i>	58	48	12	57

tion among repeated responses for each twig with the correlation dependent on the time elapsed between observations (Littell et al. 2006). However, because it was rare for marked twigs to change burial status once they were buried, the latter model (including time-correlated errors within twig responses) was not informative. Consequently, we treated plants and twigs within plants as random effects in subsequent models.

Preliminary analyses indicated that maximum plant height and basal diameter were strongly correlated measures of plant size ($r=0.73$). Because we needed only one measure in the analyses, we used plant height as our size measure in subsequent analyses. Also, we found complex relationships (i.e., multiple interactions containing continuous covariates) among snow depth, plant height, twig height, and plant architecture. Although we could analyze the data with one complex model, we found the complexity of the data could be accommodated in a more understandable way by dividing the data into 4 subsets based on the quartiles of plant height, which resulted in maximum plant height grouping subsets of ≤72 cm, 72–94 cm, 94–124 cm, and >124 cm (Table 1). Also, we included a quadratic term for twig height to account for a nonlinear response and allowed separate response functions by plant architecture (i.e., architecture × snow depth, and architecture × twig ht interactions). For each plant height subset, we began with the full model including all of the predictors, including quadratic terms and interactions, and eliminated terms from the model one at a time based on Wald *F*-statistics ($P > 0.05$), continuing until all remaining terms were important. We retained non-significant lower order terms if they were contained in significant interactions. To assess the fit of our estimated regression equations, we calculated R_G^2 , a generalized, deviance-based analog of traditional R^2 (J. M. Ver Hoef, National Marine Mammal Lab, unpublished data); R_G^2 is interpreted the same as R^2 .

To examine the biological significance of using simple

Table 2. Generalized Linear Models for data subsets based on quartiles of maximum plant height and associated level of significance. Models test for significant relationships between probability of blueberry twig biomass burial by snow and relevant independent variables. We collected data during November 2003–March 2004, Fish Creek, Alaska, USA.

Effect	Plant ht (cm)			
	≤72	73–94	95–124	>124
Snow depth (cm)	<0.001	<0.001	<0.001	<0.001
Twig ht (cm)	0.012	0.755	0.002	0.449
Twig ht (cm) ²	0.026	0.749	<0.001	0.295
Lateral vs. erect (LE)	0.003	<0.001	0.848	0.011
Snow depth (cm) × LE	<0.001	0.790	0.006	0.005
Twig ht (cm) × LE	0.006	0.896	0.987	0.032
Twig ht (cm) ² × LE	0.013	0.258	0.397	0.021

linear (i.e., ground-up) versus nonlinear models of snow burial on deer nutritional ecology, we compared estimates of deer winter nutritional carrying capacity under 2 scenarios to provide an example for how snow–shrub burial relationships can be applied in a management context and why it is important to use detailed modeling approaches. For the basis of these analyses, we used a nutritional carrying capacity model developed for Sitka black-tailed deer in Southeastern Alaska (Hanley and Rogers 1989; Hanley et al. 2006, 2007). This modeling framework uses habitat-specific forage biomass and nutritional quality information to predict number of days an adult female black-tailed deer can meet user-specified nutritional requirements in a 1-ha habitat patch. For our simulations, we used a published biomass dataset from a nearby area typical of deer winter range in northern southeastern Alaska (“old growth upland forest – stand 2”; Hanley and Hoel 1996:1706). For each simulation, we assumed that twig height distribution of blueberry plants in the biomass dataset was similar to that from our study area. Further, we assumed that forbs would be buried when snow depths were <10 cm (Hanley et al. 2007). We then calculated available (i.e., above snow) blueberry biomass (kg/ha) and consequent deer carrying capacity (deer days/ha) for a range of snow depths (i.e., 0–150 cm, at 10-cm intervals) using both the ground-up approach and based on our nonlinear regression model. For the nonlinear regression model, we estimated the proportion of biomass available at each snow depth using data from our study (including plant ht, twig ht, and plant architecture) and the estimated regression equations; we multiplied these estimated proportions by the biomass available without snow. We estimated confidence intervals for the available biomass using a parametric bootstrap. For each of the 1,000 bootstrap replicates, we calculated a random set of regression coefficients which were based on normal distributions with our estimated coefficients and their standard errors as parameters. We calculated available biomass for each snow depth with each bootstrap equation in the same way as with our original equation; for each snow depth, approximate 95% confidence bounds were the 2.5th and 97.5th values in the ordered estimates of biomass availability. Our user-specified nutritional requirements were the following:

Table 3. Coefficients (and SE) for logistic regression equations relating probability of blueberry twig burial to snow depth, plant architecture (lateral or erect), and twig height, based on data collected during November 2003–March 2004, Fish Creek, Alaska, USA. We stratified analyses by quartiles of plant height. In cases where only one coefficient for a variable is denoted (i.e., snow depth for plants between 73 cm and 94 cm) the coefficient applies to both lateral and erect plants.

Coeff.	Plant ht (cm)							
	≤72		73–94		95–124		>124	
	Value	SE	Value	SE	Value	SE	Value	SE
Y-intercept, erect	3.9856	1.8950	−3.0922	0.4635	−0.0425	1.9717	0.2175	1.8434
Y-intercept, lateral	−4.4862	1.8063	−2.1923	0.5919	−1.3479	2.8016	−4.9375	1.7029
Snow depth (cm)			0.1908	0.0090				
Erect × depth	0.1878	0.0142			0.2526	0.0122	0.1485	0.0138
Lateral × depth	0.5851	0.0643			0.4413	0.0682	0.2409	0.0295
Twig ht (cm)					−0.1410	0.0447		
Erect × twig ht	−0.3498	0.0934					−0.0752	0.0349
Lateral × twig ht	0.0199	0.0942					0.0361	0.0382
Twig ht (cm) ²					0.0010	0.0003		
Erect × twig ht ²	0.0038	0.0011					0.0004	0.0002
Lateral × twig ht ²	0.0002	0.0015					−0.0002	0.0002
R _G ²	0.66		0.55		0.68		0.52	

metabolizable energy requirement = 960 kcal/day; dry matter intake = 525 g/day; dietary digestible dry matter ≥48%, dietary digestible protein ≥1.8% (see Robbins 1993, Parker et al. 1999, Hanley et al. 2007).

RESULTS

Overall, probability of twig burial was a complex function of snow depth, plant height, plant architecture, twig height, and their interactions (Tables 2 and 3). Within this complex pattern, there were some general relationships. Probability of burial was positively related to snow depth for all analyses (Table 3) and twigs often were buried when snow depth was less than prewinter twig height, which occurred because plants tended to bend under the weight of accumulating snow. Probability of burial of median height twigs was higher on lateral plants than on erect plants (Fig. 1; Table 3). Furthermore, the shortest and tallest twigs on erect plants were more likely to be buried at any given snow depth

than were intermediate height twigs (Figs. 2a, 3a; Table 3). In contrast, all twigs, irrespective of height, had similar burial probabilities on lateral plants (Figs. 2b, 3b; Table 3) due to equal exposure of all twigs to snow accumulation.

The contrasting linear (i.e., ground-up) and nonlinear snow-burial functions we tested provided different estimates of blueberry twig biomass availability over a range of snow depths. Nonlinear estimates of blueberry twig biomass under different snow-depth scenarios indicated that twig biomass availability would be reduced to zero at snow depths >60 cm. In contrast, the linear snow-burial function estimated that 72% of blueberry biomass was still available when snow depth was 60 cm and that biomass availability was not reduced to zero until >150 cm of snow was on the ground (Fig. 4). Resulting estimates of deer nutritional carrying capacity (deer days/ha) were contingent on the snow-burial function (Fig. 5). For example when snow depth equaled 60 cm, estimated carrying capacity using the nonlinear function was zero deer days/ha, whereas the result based on a linear snow-burial function was 38 deer days/ha, or 20% of the value for snow-free conditions (i.e., 187 deer days/ha).

DISCUSSION

Understanding how environmental variation affects deer ecology is important for effective conservation and management of the species. Snow burial of woody browse can be a complex process and is influenced by factors related to snow depth, plant size, and plant architecture. We determined that whether plants have an erect or lateral growth form alters the probability that associated twig biomass will be buried by a given level of snow accumulation, which occurs because snow accumulation and persistence is greater on lateral than on erect plants due to an increased surface area exposed to snow. Further, lateral plants have a reduced ability to withstand bending under similar snow loads due to differences in geometric pressure resistance of stems. Similar to previous studies (Jenkins et al. 1990, Hovey and Harestad

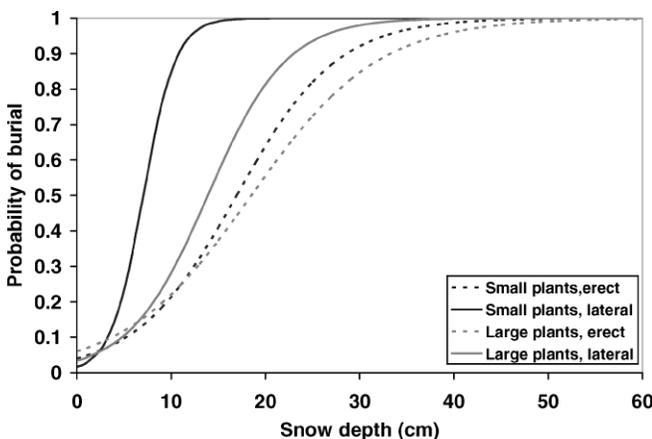


Figure 1. The relationship between probability of blueberry twig burial and snow depth for small (0–25 percentile) and large (75–100 percentile) plants of lateral and erect architecture during November 2003–March 2004, Fish Creek, Alaska, USA. Probability curves are based on median twig height for each plant category.

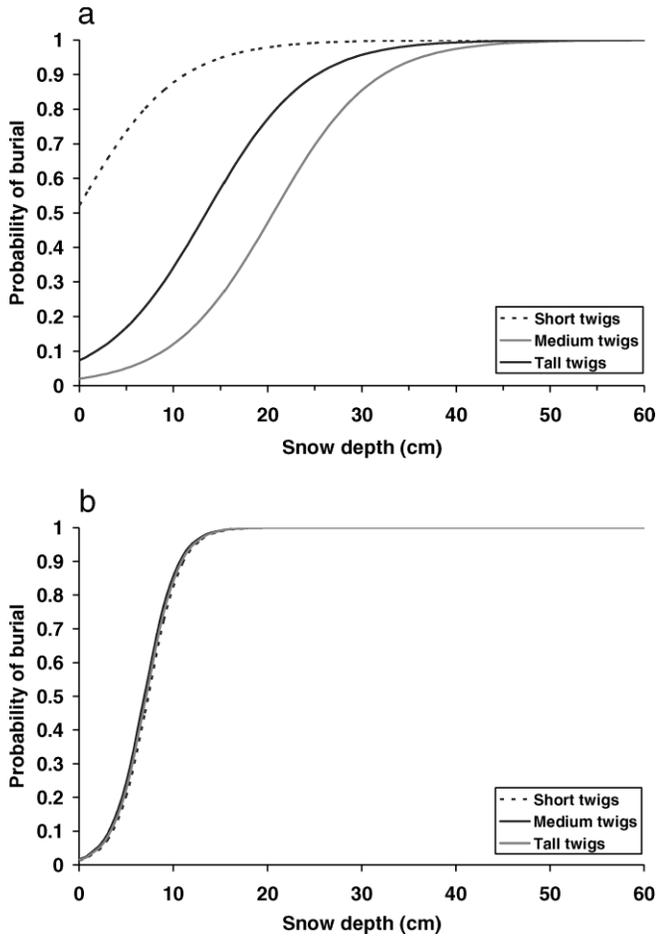


Figure 2. The relationship between probability of blueberry twig burial and snow depth for twigs at different prewinter heights on (a) erect and (b) lateral plants in the 0–25% plant-height quartile (i.e., small plants) during November 2003–March 2004, Fish Creek, Alaska, USA. Probability curves are based on minimum (11–13 cm), median (38–40 cm), and maximum (65–66 cm) twig heights for each plant category.

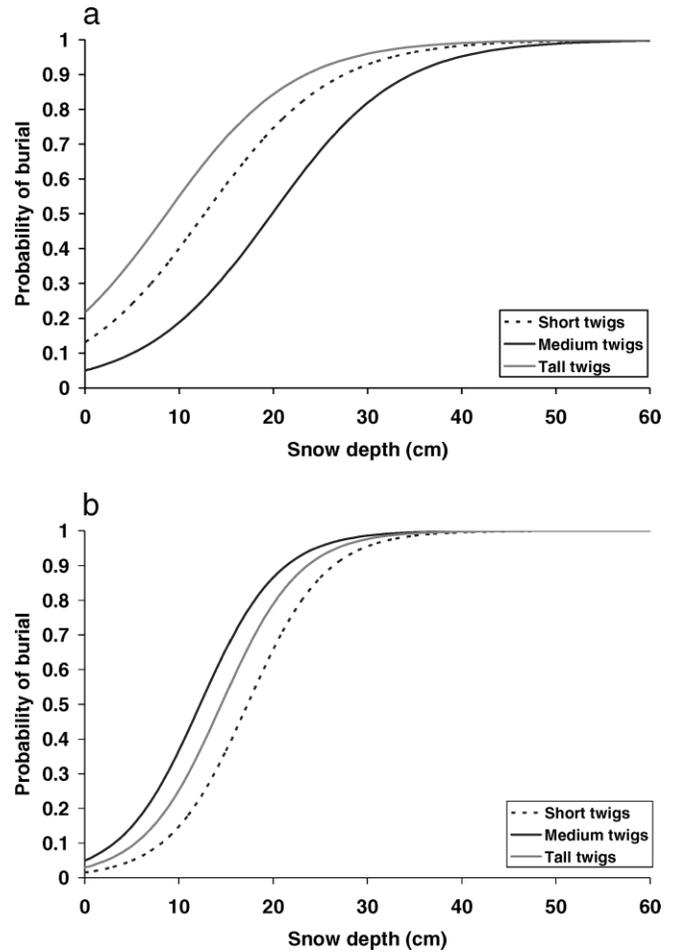


Figure 3. The relationship between probability of blueberry twig burial and snow depth for twigs at different prewinter heights on (a) erect and (b) lateral plants in the 75–100% plant-height quartile (i.e., large plants) during November 2003–March 2004 in the Fish Creek, Alaska, USA. Probability curves are based on minimum (24–35 cm), median (94–104 cm), and maximum (152–174 cm) twig heights for each plant category.

1992), we determined that height of individual plants influences probability of a twig being buried.

That snow-burial dynamics of woody browse occur in complex ways is not surprising (Schwaub et al. 1987, Jenkins et al. 1990, Hovey and Harestad 1992). Biologically, snow-burial probabilities of woody browse are best described using nonlinear regression models because shrub-tissue biomass is highly flexible and consequently prone to bending as snow accumulates on plant surfaces. Blueberry plants presumably benefit from this morphological characteristic in 2 ways. First, stem flexibility prevents plants from losing critical biomass from breakage under heavy snow accumulation. Breakage loss of live tissue negatively affects plants through loss of photosynthetic potential and plant productivity in subsequent years. Second, in snowy environments, dormant winter shrubs that are buried quickly under modest snow depths due to flexible stems would be less likely to be browsed by herbivores. Because browsing pressure can be high on critical deer winter ranges and result in negative effects on future plant productivity (Cote et al. 2004), mechanical adaptations leading to reduced herbivory may be

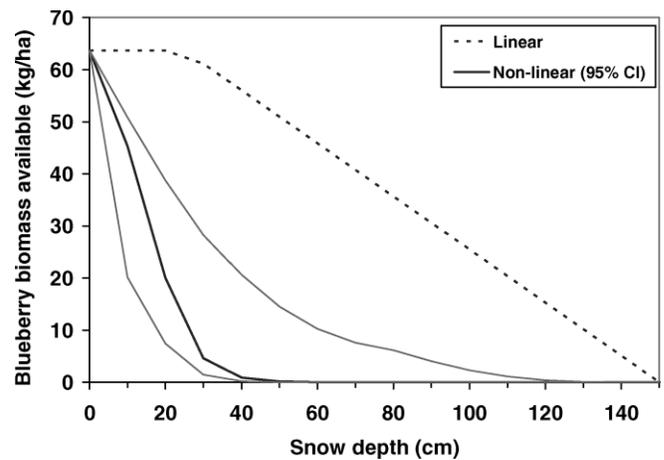


Figure 4. The relationship between blueberry biomass availability (kg/ha) and snow depth for linear (i.e., ground-up) and nonlinear (this study) snow-burial models. Based on forage biomass estimates from an upland old-growth forest stand, Kadashan, Alaska, USA (Hanley and Hoel 1996). Confidence interval estimates (95%) for nonlinear models delineated by thin gray lines.

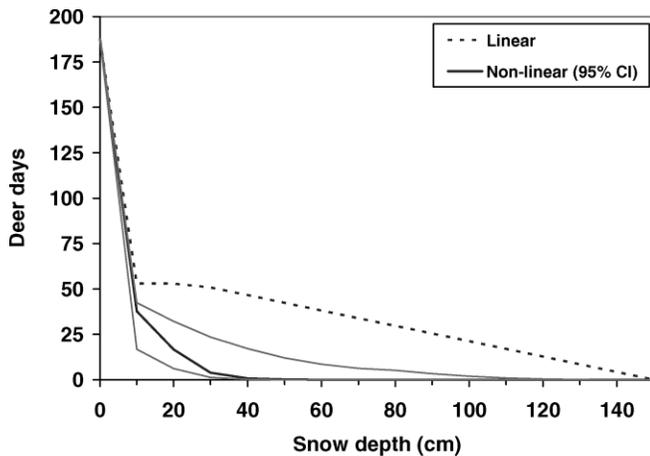


Figure 5. The relationship between estimates of Sitka black-tailed deer nutritional carrying capacity (deer days/ha) and snow depth for linear (ground-up) and nonlinear (this study) snow-burial models. Based on forage biomass estimates from an upland old-growth forest site, Kadashan, Alaska, USA (Hanley and Hoel 1996). Confidence interval estimates (95%) for nonlinear models delineated by thin gray lines.

of adaptive significance. Understanding processes that influence shrub burial by snow will be important for future studies that involve shrub forages other than those we described, particularly in cases where plant morphologies are different.

Our winter-browse availability and deer nutritional carrying capacity model simulation analyses underscore the biological significance of using nonlinear models for characterizing snow-burial dynamics in northern coastal ecosystems. Our simulations indicated that estimates of winter availability of blueberry browse and Sitka black-tailed deer nutritional carrying capacity can be greatly overestimated if linear, ground-up models of snow burial are used instead of nonlinear models, such as those described herein. Nonetheless, it is important to recognize that forage-plant composition and physical characteristics of snow vary across biogeographic provinces and applicability of our findings may vary accordingly. For example, Hobbs (1989) found that linear models of shrub burial by snow were adequate for linking energy balance to survival of deer in shrub-steppe ecosystems. Thus, it is important to recognize that accurate modeling of deer nutritional landscapes must consider local factors that influence snow-burial dynamics of important winter forages.

The models we used integrate burial probabilities of shrub biomass across a range of snow conditions. In high-latitude maritime snow climates, alternating periods of above- and below-freezing temperatures are common and snow stratigraphy can be complex and regularly show characteristics associated with both maritime and continental snow climates (Hood et al. 2005). As a result, the character of snow-burial processes in this region is relatively complex, as compared to more southerly and interior snow climates. It is also important to recognize that distinct weather events within a given winter period (e.g., alternating periods of snow accumulation and ablation) may influence shrub burial

processes in ways we did not explicitly address. Nonetheless, general models that integrate burial probabilities across an entire winter are useful for most practical applications, because detailed site-specific monitoring of snow conditions is not often possible.

MANAGEMENT IMPLICATIONS

In northern coastal ecosystems winter snow accumulation is considered to be an important driver of deer population dynamics (Klein and Olsen 1960, Patterson and Power 2002). The nonlinear models described in this study indicate that the nutritional carrying capacity of upland old-growth forest habitats is extremely limited when snow exceeds 30 cm in depth. At such depths, the energetic costs of movement also increase significantly (Parker et al. 1984). Consequently, under conditions similar to this study, resource managers should consider snow depths >30 cm to represent a winter severity threshold above which deer should be expected to be nutritionally and energetically stressed. When threshold values are exceeded, deer population management strategies should be adjusted to account for expected declines in deer nutritional condition and ensuing impacts on population productivity and over-winter mortality.

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