Scale-dependent drivers of ungulate patch use along a temporal and spatial gradient of snow depth

J.C. Witt, C.R. Webster, R.E. Froese, T.D. Drummer, and J.A. Vucetich

Abstract: Anthropogenic changes in landscape composition or configuration have the potential to increase the abundance of generalist species, often resulting in cascading effects on other trophic levels and ecosystem function. The selection or utilization of individual patches of habitat, however, may vary in both time and space, as a result of patch and landscape attributes as well as dynamic abiotic factors (i.e., snowfall). We hypothesized that the use of high-quality habitat would be most strongly influenced by snow at local scales and by composition and the configuration of the landscape at greater spatial scales. To test this, we examined white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)) selection of eastern hemlock (*Tsuga canadensis* (L.) Carrière) patches as winter habitat over a 3-year period. Patch-level attributes were poor predictors of patch use in areas with strong gradients in abiotic factors relevant to the energetics of movement or forage acquisition. Additionally, heterogeneity in the greater landscape (3000 m radius buffer) served to increase use, while homogeneity appeared to decrease use. Our results suggest that interactions between deer migratory behavior, interannual variation in winter severity, and landscape context might provide spatial and temporal refugia for hemlock regeneration; a better understanding of which could aide conservation and restoration.

Key words: eastern hemlock (*Tsuga canadensis*), FRAGSTATS, generalized linear model, habitat selection, white-tailed deer (*Odocoileus virginianus*), Upper Peninsula of Michigan, winter cover.

Résumé : Les changements d'origine anthropique de la composition ou de la configuration du paysage peuvent accroître l'abondance d'espèces généralistes, ce qui se traduit souvent par des effets de cascade sur d'autres niveaux trophiques et sur la fonction de l'écosystème. La sélection ou l'utilisation de parcelles d'habitat données peut toutefois varier dans le temps et dans l'espace en raison des attributs des parcelles et du paysage ainsi que de facteurs abiotiques dynamiques (c.-à-d. des chutes de neige). Nous avons postulé que les facteurs exerçant la plus grande influence sur l'utilisation d'habitats de bonne qualité sont la neige aux échelles locales et la composition et la configuration du paysage à de plus grandes échelles spatiales. Pour tester cette hypothèse, nous avons examiné la sélection par le cerf de Virginie (*Odocoileus virginianus* (Zimmermann, 1780)) de parcelles de pruches du Canada (*Tsuga canadensis* (L.) Carrière) comme habitat hivernal sur une période de trois ans. Les attributs au niveau de la parcelle ne se sont pas avérés être de bons paramètres prédictifs de l'utilisation d'habitat dans les zones présentant de forts gradients de facteurs abiotiques importants pour l'énergétique des déplacements ou de l'acquisition de nourriture. En outre, dans le plus grand paysage (zone tampon d'un rayon de 3000 m), l'hétérogénéité était associée à une utilisation accrue alors que l'homogénéité semblait réduire l'utilisation. Nos résultats portent à croire que les interactions entre le comportement migratoire des cerfs, la variabilité interannuelle de la rigueur de l'hiver et le contexte du paysage pourraient fournir des refuges dans l'espace et dans le temps pour la régénération des pruches. Une meilleure compréhension de ces interactions pourrait être utile pour la conservation et la restauration.

Mots-clés : pruche du Canada (*Tsuga canadensis*), FRAGSTATS, modèle linéaire généralisé, sélection d'habitat, cerf de Virginie (*Odocoileus virginianus*), péninsule nord du Michigan, couverture hivernale.

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Introduction

Wildlife species that are able to survive and reproduce in highly fragmented landscapes respond to patchiness in their environment across a range of spatial and temporal scales (Wiens 1976; Senft et al. 1987). For ungulates, selection of habitat may begin at the coarser scale of a home range or migration route and be further honed by behaviors at finer spatial scales (Johnson 1980). Processes that influence habitat selection at one scale, however, are not necessarily the same as those that are influential at another (Senft et al. 1987; Turner 1989). At the coarser scale of a landscape, an increase

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in patchiness or edge has been shown to be influential in the selection of both winter and summer ranges for elk (*Cervus elaphus* L., 1758) (Jones and Hudson 2002; Boyce et al. 2003). Home-range sizes of mule deer (*Odocoileus hemionus* (Rafinesque, 1817)) tend to be smaller in highly heterogeneous landscapes (Kie et al. 2002). At finer scales, the spatial arrangement of vegetation can influence ungulates as they utilize cover, select forage, and avoid predators (Pearson et al. 1995; Rettie and Messier 2000; Johnson et al. 2002). However, habitat selection at one scale may be impeded by limits to selection at another, and these hierarchical constraints, as well as scales of influence, are still being debated (Mayor et al. 2009).

Perhaps one of the best-known examples of a species that has been able to thrive in heterogeneous or fragmented landscapes is the white-tailed deer (*Odocoileus virginianus* (Zimmermann, 1780)), as landscapes interspersed with large amounts of forested edge, agriculture, and early-successional habitat provide abundant forage and cover for this generalist species (Dahlberg and Guettinger 1956; Alverson et al. 1988; Waller and Alverson 1997; Millington et al. 2010; Hurley et al. 2012). Additionally, a lack of predators and hunting laws geared toward protecting deer populations have contributed to high deer densities and range expansion, and in some regions of eastern North America, deer are thought to be locally overabundant or at densities that exceed social or ecological carrying capacity (McShea et al. 1997; Rooney 2001). White-tailed deer, like many ungulates, have the ability to influence plant community distribution and abundance (Alverson et al. 1988; Waller and Alverson 1997; Rooney 2001, 2009; Webster et al. 2008). Throughout their distribution, numerous studies have and continue to document how locally overabundant deer populations are directly or indirectly causing shifts in or homogenization of plant populations and communities, which have, in turn, led to cascading effects on animal species and ecosystem processes (e.g., McShea et al. 1997; Russell et al. 2001; Côté et al. 2004; Holmes and Webster 2011; but see Rutherford and Schmitz 2010).

Adding to the influence of landscape heterogeneity, seasonal weather events also have the potential to modify or decrease the quality or availability of habitat (Turner 1989). Throughout the Upper Great Lakes region, winter severity is thought to be one of the major factors limiting regional populations of white-tailed deer (Xie et al. 1999). Deer respond to harsh winter conditions by congregating in areas of dense conifer cover, which are thought to provide refuge from heavy snow, high winds, and radiant heat loss, as well as lower snow for ease of movement and predator avoidance (Blouch 1984; Nelson and Mech 1981, 1991; Nelson and Mech 2006). When available, eastern hemlock (*Tsuga canadensis* (L.) Carrière) stands are preferentially utilized as winter "yarding" habitat across the region (Verme 1973; Euler and Thurston 1980). Contemporary hemlock abundance, however, exists at just a fraction of its pre-European settlement amount (reduced to only 0.5% of its former range in the Great Lake states; Mladenoff and Stearns 1993; Whitney 1987), and it is often found in small, remnant patches surrounded by a landscape dominated by second-growth deciduous forests (Alverson et al. 1988). Deer numbers, on the other hand, are thought to be at least double those of pre-European settlement times (Doepker et al. 1994). The brows-

ing pressure placed on hemlock during winter is thought to be one of the major factors limiting hemlock recruitment across the region (Frelich and Lorimer 1985; Alverson et al. 1988; Rooney et al. 2000; Witt and Webster 2010; Salk et al. 2011). Because yarding traditions are learned and maintained by social ties (Nelson and Mech 1981; Van Deelen et al. 1998), the absence of hemlock regeneration and other browse typically does not result in yard abandonment or selection of alternate habitat (Euler and Thurston 1980). Variation in winter severity, however, may result in incomplete or conditional migration (Nelson 1995; Van Deelen et al. 1998) and variation in within-yard habitat selection (Morrison et al. 2003).

The distribution of hemlock is limited and patchy across the landscape, yet despite hemlock's low abundance and high desirability as winter habitat, remnant patches are not used uniformly by wintering deer. Some patches are experiencing high levels of use, whereas others appear unused. Seasonal and yearly snowfall across the region tends to be high and highly variable, owing to the climatic influences of Lake Superior (Eichenlaub 1970). As snow depth has been shown to influence habitat selection (Morrison et al. 2003), we expect that variation in snow depth will be an important factor influencing hemlock patch use. Additionally, across the region, many of these remnant patches are surrounded by a dominant cover of second- and third-growth deciduous forests. This could influence patch discovery by dispersing deer (establishment of a yarding tradition) and the persistence of the yarding population. Because the fitness of the deer population is, in part, linked to this winter habitat, we expect that both the quality of that habitat and its availability within the landscape will be influential to individual patch use. A better understanding of winter habitat use could aide managers in identifying remnant stands suitable for regeneration and restoration treatments to help ensure the maintenance and perpetuation of this important cover type.

The objective of this study was to test the importance of scale in identifying how local-scale factors (within patch: e.g., snow depth, forage availability, quality of winter cover) and the structure of the landscapes surrounding hemlock patches influence patch use by wintering deer. We hypothesize that quality of winter cover (as indicated by hemlock basal area; Euler and Thurston 1980; Lang and Gates 1985) will be more important in high snow years, whereas in lower snow years deer use will be greater in patches with greater forage availability as a result of incomplete migration, transient use, and (or) early departure from traditional winter yards. However, given that scale-specific habitat decisions are often an indication of the risk–reward trade-off to fitness (Mayor et al. 2009), we expect that the composition and the configuration of the greater landscapes surrounding high-quality habitat will also influence habitat use (Hurley et al. 2012).

Materials and methods

Our study area was located in the western Upper Peninsula of Michigan, on the south side of Lake Superior in the Laurentian Great Lakes region (Fig. 1). Using US Forest Service and Michigan Department of Natural Resources inventory data, we selected a stratified random sample of 39 remnant eastern hemlock patches from strata defined by four levels of

Fig. 1. Western Upper Peninsula of Michigan study area (left) with land-cover types of "conifer", "deciduous", "open", and background as reclassified from IFMAP and WISCLAND 30 m × 30 m resolution land-cover data. Insets (middle) are close-ups of eastern hemlock (*Tsuga canadensis*) study patches with concentric circles representing 500, 1000, 3000, 5000, and 7000 m buffers surrounding patch. Aerial photos (right; photographs by R.L. Anderson) depict hemlock study patches (outlined in white) and the surrounding snow-covered landscape. Letters indicate specific study patches and their locations within the study area.
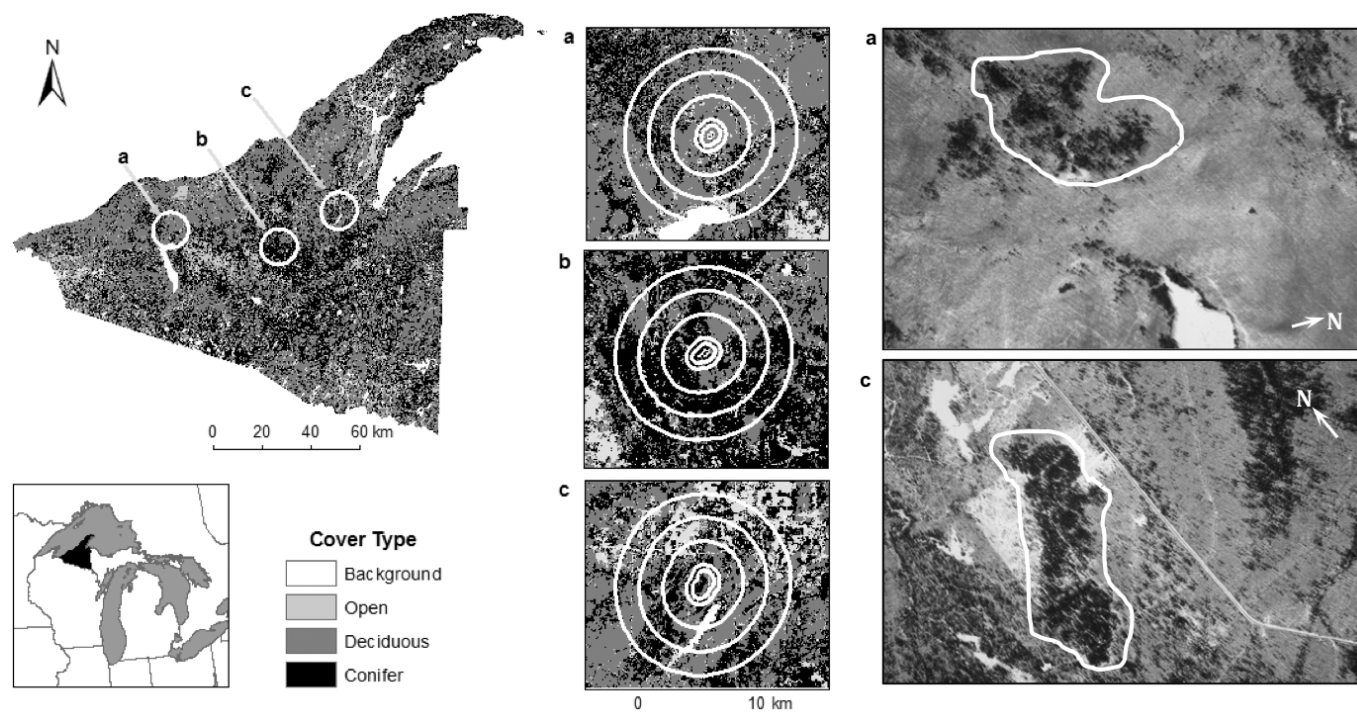
patch area and high or low relative snow depth. Patches ranged in size from 0.4 to 60 ha. The size of the winter range varies greatly between years in northern Michigan depending on winter severity. During a 3-year telemetry study, Van Deelen et al. (1998) observed mean annual winter range sizes of 730, 804, and 1859 ha during a series of mild winters. Consequently, these hemlock patches likely represent a small but important part of the winter range. With deer use as our response variable, we used a generalized linear modeling framework to test our hypotheses about the relationship between use of remnant hemlock patches and patch- and landscape-scale explanatory variables on an annual (patch-scale only) and multiyear basis.

To quantify the intensity of winter deer use for each of the remnant hemlock patches, we conducted yearly counts of fecal pellet groups for each patch. Study sites contained randomly placed circular pellet-group plots (5, 10, 20, or 30, depending on patch size) with a sampling area of 9.29 m^2 (1.72 m radius). Plots were cleared of pellets prior to the first winter, and immediately following snow melt, pellet groups were counted by a two-person team employing a system of concurrent rechecks. Concurrent rechecks were conducted by dividing the plot in half and having each observer simultaneously count the number of pellet groups in their half and then switch and count pellet groups in the other observer's half. The final count was then confirmed by both observers. Deer use was quantified for each study patch for winters 2005–2006, 2006–2007, and 2007–2008.

At the patch scale, we quantified habitat through direct measures of hemlock patch composition and structure. We used hemlock basal area as an indicator of the quality of winter cover (Telfer 1970). Overstory and mid-story (stems ≥4 cm diameter at breast height (DBH)) composition and structure were measured on randomly placed 400 m^2 circular plots (3, 5, 7, or 9 plots, depending on patch size). The availability of winter forage for each study patch was quantified on three 1 m × 10 m, randomly oriented, parallel belt transects embedded within each overstory circular sampling plot. Although historically hemlock was likely an important winter browse species, regeneration of this species has been absent from many stands in the region for decades (Maissurow 1941; Anderson and Loucks 1979; Rooney and Waller 1998). This is due in part to the high sensitivity of this species to browse, especially in shaded understory environments where herbivory appears to contribute to the replacement of this species by the more palatable and less browse sensitive sugar maple (*Acer saccharum* Marsh) (Anderson and Loucks 1979; Anderson and Katz 1993; Witt and Webster 2010; Jensen et al. 2011). Although maple abundance varies widely in hemlock stands (Witt 2010), given the comparative rarity of hemlock regeneration, sugar maple in particular has been commonly used to assess browse pressure (Frelich and Lorimer 1985; Rooney et al. 2000). Therefore, we used maple (sugar maple and red maple (*Acer rubrum* L.)) stem density for stems 0.25 cm in height to 0.1 cm DBH (~1.5 m in height) as an indicator of within-patch forage availability.

Additional patch-scale variables of snow depth, elevation, and patch area were derived using GIS and remotely sensed data. We calculated mean winter snow depth using Snow Data Assimilation System (SNODAS) data, a 1 km snow

Table 1. Local- and landscape-scale variable codes, description, units, and source of data used to model eastern hemlock (*Tsuga canadensis*) patch use by wintering white-tailed deer (*Odocoileus virginianus*).

Scale	Code	Variable name	Source, metric description, and (or) units
Snow			
Local	SN	Mean snow depth	NOHRSC-SNODAS 2004 (m)
Local	SN-SE	Mean snow depth standard error	NOHRSC-SNODAS 2004 (m)
Local	ELE	Elevation	90 m digital elevation model (DEM) (m)
Cover			
Local	AREA	Eastern hemlock stand size	Stands selected using USDA Forest Service forest-type data 1998 and digitized using USGS digital orthophotos 1998 (ha)
Local	HEM_BA	Basal area eastern hemlock	Field measurement ($m^2 \cdot ha^{-1}$)
Local	HEM_Pct	Eastern hemlock percentage of total basal area	Field measurement (%)
Browse			
Local	BROWSE	Available browse: *Acer* spp. (stems 0.25 m in height to 0.1 cm diameter at breast height (DBH))	Field measurement (no. of stems·ha^{-1})
Landscape*			
Patch area, shape, and edge metrics			
Landscape	Pct	Percent cover	Percentage of landscape
Landscape	NP	Number of patches	Number of patches
Landscape	PD	Patch density	Number of patches divided by buffer area
Landscape	LP	Largest patch index	Percentage of landscape occupied by the largest patch
Landscape	Edge	Total edge	Length of edge
Landscape	ED	Edge density	Length of edge divided by buffer area
Landscape	Mn	Mean patch size	Mean patch size
Landscape	AM	Area-weighted mean patch size	Mean patch size divided by buffer area
Landscape	Md	Median patch size	Median patch size
Landscape	SD	Patch size standard deviation	Standard deviation of patch size
Landscape	CV	Patch size coefficient of variation	Standard deviation of patch size divided by mean patch size
Landscape	Shape	Landscape shape index	Total length of edge divided by minimum possible total length of edge
Connectivity, fragmentation, and heterogeneity metrics			
Landscape	Adj	Percentage of like adjacencies	Measure of dispersion of cover type. Decreasing values indicate a increasing disaggregation of cover type
Landscape	Clump	Clumpiness index	Measure of dispersion of cover type scaled for proportion of landscape occupied by patch type. Values range from –1 > clump < 1, where a value of zero indicates randomly dispersed patches of indicated cover type. Lower values indicate more disaggregated, whereas higher values indicate higher aggregation
Landscape	Coh	Patch cohesion index	Measure of physical connectedness of indicated cover type. Increasing values of cohesion indicate a more physically connected cover type
Landscape	Div	Patch division index	Measure of patchiness of cover type. Increase in proportion indicates a decrease in connectedness
Landscape	Agg	Aggregation index	Measure of dispersion of specified cover type. Higher values indicate a greater level of aggregation
Landscape	Split	Splitting index	Measure of patchiness of cover type. Split increases as the cover type is divided into smaller pieces
Landscape	IJI	Interspersion and juxtaposition index	Measure of patch adjacency. Higher values indicate uneven adjacency for indicated cover type, while lower values indicate that all patches are equally adjacent

Note: Landscape metrics were calculated in FRAGSTATS (McGarigal et al. 2002) using Michigan IFMAP/GAP land-cover data 2001 (Michigan Department of Natural Resources 2001) and WISCLAND land-cover data 1998 (Wisconsin Department of Natural Resources 1998).

*Landscape variables modified by cover type: conifer (CON), deciduous (DEC), open (OPEN), or patches of all cover types (conifer, deciduous, and open) within a buffer (ALL). For a more thorough description of landscape metrics see McGarigal et al. 2002.

Table 2. Descriptive statistics for patch-level variables used to model eastern hemlock (*Tsuga canadensis*) patch use by wintering white-tailed deer (*Odocoileus virginianus*).

Code	Variable	Mean	SD	Minimum	Maximum
Snow					
SN					
Winter 2005–2006	Mean snow depth (m)	0.33	0.11	0.08	0.51
Winter 2006–2007		0.25	0.07	0.15	0.46
Winter 2007–2008		0.43	0.09	0.28	0.64
SN-SE					
Winter 2005–2006	Standard error of mean snow depth (m)	0.015	0.004	0.006	0.023
Winter 2006–2007		0.018	0.004	0.010	0.025
Winter 2007–2008		0.013	0.003	0.009	0.018
Snow					
AREA	Stand area (ha)	14.4	14.1	0.04	59.6
HEM_BA	Eastern hemlock basal area ($m^2 \cdot ha^{-1}$)	24.0	12.1	8.0	57.6
HEM_Per	Eastern hemlock percentage of overstory	51.9	16.9	21.4	85.4
ELE	Elevation (m)	405.3	109.7	186.3	555.7
Browse					
BROWSE	Browse available: *Acer* spp. (no. of stems·ha^{-1})	3 589	6 162	0	31 500

Note: See Table 1 for a description of the codes.

Fig. 2. Mean seasonal snow depth (15 December – 15 March) for the study periods, winter 2005–2006, 2006–2007, and 2007–2008 (National Operational Hydrologic Remote Sensing Center 2004). Red circles indicate relative patch use (no. of pellet groups·ha^{-1}) of eastern hemlock (*Tsuga canadensis*) patches by wintering white-tailed deer (*Odocoileus virginianus*) as determined by after snowmelt pellet group counts.
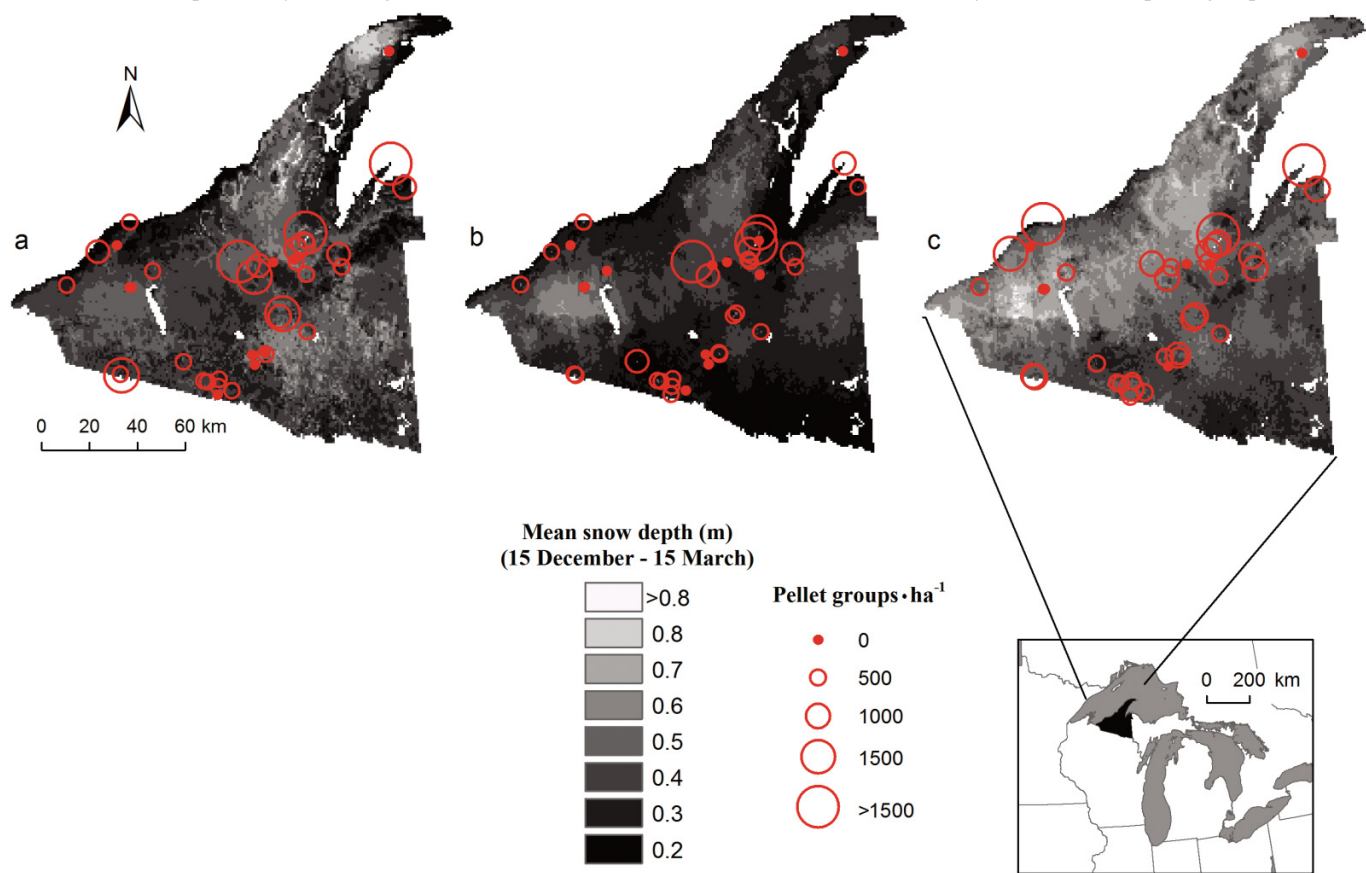
Table 3. Descriptive statistics of white-tailed deer (*Odocoileus virginianus*) fecal pellet groups·ha^{-1} deposited annually in the 39 eastern hemlock (*Tsuga canadensis*) study patches located throughout the western Upper Peninsula of Michigan, USA.

Year	Number of pellet groups·ha^{-1}			
	Mean	SD	Minimum	Maximum
2005–2006	496	614	0	2296
2006–2007	282	423	0	1722
2007–2008	504	528	0	2260

simulation model data set derived from daily satellite, aerial, and ground-based observations (National Operational Hydrologic Remote Sensing Center (NOHRSC) 2004). Daily snow conditions were averaged for the 15 December – 15 March sampling period to calculate a seasonal mean and variance for snow depth at each study site. Patch elevation was derived from a 1 : 250 000 scale digital elevation model for Michigan. Because study sites selected for this study were initially defined by legal boundaries associated with ownership, to obtain a more accurate measurement for patch area independent of ownership we digitized hemlock patches from US Geological Survey (USGS) digital orthophoto quadrangles (US Geological Survey 1998) using ArcGIS version 9.2 (Environmental Systems Research Institute (ESRI) Inc., Redlands, California, USA).

To assess the influence of the landscape on hemlock patch use surrounding each study site, we established 500, 1000, 3000, 5000, and 7000 m concentric buffers from the edge of each hemlock patch (Fig. 1). These buffer distances were selected based on observed differences between harmonic mean centers of winter and summer ranges (3-year mean = 7.29 km) reported by Van Deelen et al. (1998) for two northern Michigan deer yards. Shorter distances likely encompass the summer and winter range of nonmigratory deer, while longer distances likely include a greater portion of the summer range of migratory deer. Within each of these buffers, we reclassified the landscapes into broader categories of "conifer", "deciduous", and "open" cover using 30 m resolution land-cover data (Fig. 1; Wisconsin Department of Natural Resources 1998; Michigan Department of Natural Resources 2001). Forested patches were reclassified as conifer or deciduous, depending on the composition of the overstory. If conifer species occupied >40% of the dominant crown cover, it was reclassified as conifer. Areas that contained <25% tree cover were considered to be open land, with the exception of aquatic and urban areas, which were classified as inaccessible background. We used FRAGSTATS (McGarigal et al. 2002) to quantify the composition and configuration of the landscapes within each of our five concentric buffers surrounding the study patch (Table 1). Metrics were chosen a priori as those that are most likely to have biological significance to white-tailed deer winter habitat selection. Specifically, we chose metrics that quantified area, edge, fragmentation, and connectivity of our three cover types, as well as the landscape as a whole (Dahlberg and Guettinger 1956; Alverson et al. 1988; O'Brien et al. 2006).

To identify factors influencing winter use of hemlock patches, we used count (number) of pellet groups per study patch as our response variable and local (snow, cover, and browse) and landscape (e.g., edge, fragmentation, and connectivity) variables as our predictor variables in a model-building process (Table 1). We hypothesized that patch-scale attributes influencing deer winter use would vary as a function of the mean depth and within-season variability in snow. To capture this variation, we modeled patch use both annually and across multiple years. Because our response variable represented count data, which we assumed followed a Poisson distribution, we used a generalized linear modeling (GLM) framework with a log-link to construct our models (Guisan and Zimmermann 2000). Also, because sampling effort was a function of patch size (i.e., larger patches had a greater number of sample plots), it was necessary to include an offset in our model (offset = log(plots)). To account for autocorrelation in the multiyear model, we included patch as a random effect in the model intercept (Schabenberger and Pierce 2002). Model parameters were estimated using maximum likelihood and all model fitting was performed in the R statistical environment, using the lme4 package (R Foundation for Statistical Computing, Vienna, Austria; Bates and Sarkar 2006).

We evaluated our hypotheses using a hierarchical set of alternative models (Burnham and Anderson 2002; Zuur et al. 2009). First, we identified a priori alternative annual and multiyear models using within-patch cover, browse, and snow variables. Using Akaike's information criterion (AIC), we identified the most parsimonious and biologically meaningful model of deer use at the patch scale, hereafter referred to as our "patch-scale" model.

To evaluate the influence of the landscape on patch use, we compared patch-scale models that were augmented with landscape metrics at each spatial extent. As many metrics were similar, we a priori grouped those that were highly correlated ($|r| \geq 0.6$) to develop proxy categories. Again using AIC, we identified the most parsimonious and biologically meaningful model for deer use, hereafter referred to as our "patch + landscape" scale model. Finally, we evaluated all of the possible landscape metrics, post hoc, to find the individual variable within the class of correlated metrics that resulted in the best improvement in model AIC score (Riitters et al. 1995; Woolf et al. 2002; Zuur et al. 2009). We treat these results more cautiously, because of the increased risk of obtaining spurious results in post hoc analyses (Burnham and Anderson 2002).

Results

Snow conditions across study patches were highly variable both on an inter- and intra-annual basis. Mean annual snow depth across all sites was 0.33, 0.25, and 0.43 m for the 2005–2006, 2006–2007, and 2007–2008 winters, respectively (Table 2). Likewise, the number of hemlock patches used by wintering white-tailed deer varied between years, with 29, 27, and 32 of the 39 patches being used during consecutive winters, respectively (Fig. 2). Relative patch use was quite variable by study site; in some patches in excess of 1500 pellet groups·ha^{-1} were deposited annually (Table 3). Within a given year, the relationship between patch use and patch attributes was influenced by year to year variation in snowfall, with browse availability less important in high snowfall years (Table 4).

Table 4. Parameter estimates and Akaike's information criterion (AIC) scores for annual versus null (intercept-only) models of eastern hemlock (*Tsuga canadensis*) patch use by wintering white-tailed deer (*Odocoileus virginianus*).

Winter	Model	Parameter estimates					AIC
		Intercept	ELE	SN	AREA	BROWSE	
2005–2006	I	0.46	–0.0046		0.022	0.000032	313.5
	Null	–0.5					502.9
2006–2007	II	0.49	–0.0060		0.014	0.000044	218.8
	Null	–1.2					345.9
2007–2008	III	2.34	–0.0055	–3.2	0.021		242.3
	Null	–0.7					372.1

Note: See Table 1 for a description of the patch-scale variables ELE, SN, AREA, and BROWSE.

For our multiyear model of winter patch use, elevation, snow, and patch area were the variables most strongly associated with deer use at the patch scale (Table 5). Parameter estimates indicate that patch use was negatively associated with patch elevation. The response to snow depth was parabolic in nature, with patch use increasing with an increase in mean annual snow depth to 38 cm before dropping off again (Fig. 3). Intra-annual variation in snow depth (standard error of snow depth) was negatively associated with patch use. Additionally, patch use increased with an increase in patch area.

Patch-scale variables for cover were not significantly associated with patch use, at least within the range of our data. Patch basal area ranged from 33.8 to 68.7 m²·ha⁻¹, with hemlock accounting for 21%–84% of the overstory basal area (Table 2). Maple browse, as an indicator of forage availability, was a good predictor in two out of three years (2005–2006 and 2006–2007) in our annual models of patch use. Browse, however, was not a good predictor in our multiyear model. Patches with browse exceeding 5000 stems·ha⁻¹ were found to have high deer use, though patches depauperate of available forage were also used as winter habitat.

For the multiyear patch + landscape models, we were able to identify alternative models of patch use in four out of five buffer distances (Table 5). Within each buffer we retained all models within six units of AIC$_{min}$, because empirical evidence may exist in support for alternative models (Burnham and Anderson 2002). Scale of influence was most apparent in 3000 and 5000 m buffers, where there was a decrease in excess of 13 AIC units from the patch-scale model (Table 5). Landscape attributes proximate to the patch, however, had little or no influence over patch use (i.e., 500 and 1000 m buffers).

Snow and elevation variables included in our multiyear patch-scale model were important predictors in all patch + landscape models, and patch area was significant in all but two of the retained models (Table 5). At the larger extent, greater buffer distances and the addition of measures of habitat fragmentation resulted in models that were better predictors of patch use than the patch-scale model. Parameter estimates for division (Div-ALL, DEC) and interspersion and juxtaposition of the open cover (IJI-OPEN) type in the 3000 and 5000 m buffers suggest an increase in patch use with a decrease in patch adjacency or connectivity (Table 5). Overall, the two models that best explain our response variable were models V and VI in the 3000 m buffer. Although both include the IJI-OPEN index, model VI shows a negative association with mean patch size of deciduous cover type (Mn-DEC), an indicator of homogeneity in the landscape. At our

coarsest scale, 7000 m buffer, hemlock patch use decreased with increasing percentage of the landscape occupied by the largest patch in the landscape (LP-DEC, ALL).

Discussion

Our results suggest that, when trying to understand and manage for a highly mobile generalist species on a regional scale, direct measures of underlying behavioral mechanisms, i.e., selection of winter habitat, may provide less information on patch use than measures that also include composition, structure, and configuration of the landscape surrounding the patch of interest. Across years, snow depth and elevation were the main drivers of patch use at all scales. However, when we moved to a scale beyond that which would include winter behavior of white-tailed deer, a scale that likely encompasses the summer range of deer in northern Michigan (~2110 ha; Van Deelen et al. 1998), we had a positive accumulation of explanatory information with the inclusion of measures of landscape composition and configuration. Our best-fit models of patch use were found at the 3000 m spatial scale, where heterogeneity in the landscape, or the lack thereof, was significantly associated with use of hemlock patches as winter habitat.

Habitat selection takes place at hierarchical spatial scales (Wiens 1976; Johnson 1980), but it remains unclear which of these scales are most influential to patch use. Our results were consistent with landscape-scale studies of ungulate habitat selection where heterogeneity had a positive influence on patch use (Kie et al. 2002; Boyce et al. 2003; Mayor et al. 2007; Hurley et al. 2012). Our best-fit models, however, were those at the greatest spatial scales, buffer widths in excess of 3000 m, and an area of influence that far exceeds what previous studies suggest to be the maximum home-range size for white-tailed deer on their wintering grounds (Tierson et al. 1985; Beier and McCullough 1990; Van Deelen et al. 1998). Conversely, proximate landscapes, those within 1000 m of the hemlock patch, had little influence over patch use. Though we do know that the composition and structure of the landscape in close proximity to winter conifer cover is important for white-tailed deer (Morrison et al. 2003), our results suggest that habitat selection is being influenced, initially, at a much greater spatial scale.

Although habitat characteristics influence habitat selection at all spatial scales, it has been hypothesized that it is the greatest spatial scales that limit the fitness of a population or individual and therefore also limit habitat use (Rettie and

Table 5. Parameter estimates, Akaike's information criterion (AIC), ΔAIC, and Akaike weights (ω_i) listed by buffer distances for multiyear patch and patch + landscape scale models of eastern hemlock (*Tsuga canadensis*) patch use by wintering white-tailed deer (*Odocoileus virginianus*).

| | Parameter estimates | | | | | | | | | | | | | | | |
Model	Intercept	ELE	SN	$(SN)^2$	SN-SE	AREA	CV-DEC	Mn-DEC	IJI-OPEN	Div-DEC	Div-ALL	LP-DEC	LP-ALL	AIC	ΔAIC	ω_i
Patch scale																
I	−1.0	−0.0049	9.75	−13.04	−37.64	0.029								296.7	18.7	0.00
500 m buffer: patch + landscape																
II	−1.8	−0.0044	9.8	−13.03	−35.88		0.004							294.8	16.8	0.00
1000 m buffer: patch + landscape																
No variables in addition to the stand-scale model were significant in this buffer																
3000 m buffer: patch + landscape																
III	0.6	−0.0066	9.4	−12.45	−35.23	0.021		−0.077						283.7	5.7	0.03
IV	−3.9	−0.0052	9.53	−12.55	−33.89	0.025					4.13			282.5	4.5	0.04
V	−8.2	−0.0056	9.4	−12.46	−35.91	0.017			0.058		3.09			278.0	0.0	0.51
VI	−5.7	−0.0063	9.29	−12.34	−36.31			−0.057	0.071					279.3	1.3	0.27
5000 m buffer: patch + landscape																
VII	−3.9	−0.007	9.42	−12.43	−34.53	0.025				4.397				281.7	3.7	0.08
IX	−4.3	−0.0058	9.7	−12.74	−33.09	0.023					4.79			282.4	4.4	0.06
7000 m buffer: patch + landscape																
X	0.7	−0.0071	9.58	−12.66	−34.58	0.025						−0.028		288.5	10.5	0.00
XI	0.3	−0.0055	9.77	−12.87	−33.80	0.028							−0.03	289.6	11.6	0.00

Note: See Table 1 for a description of the patch-scale variables ELE, SN, SN-SE, AREA, CV-DEC, Mn-DEC, IJI-OPEN, Div-DEC, Div_ALL, LP-DEC, and LP-ALL.

Fig. 3. Predicted white-tailed deer (*Odocoileus virginianus*) pellet groups per hectare for multiyear patch-scale model as a function of mean snow depth and elevation. Plots depict predicted values at three levels of eastern hemlock (*Tsuga canadensis*) patch area as determined by 25%, 50%, and 75% quartiles within the range of our data: (left panel) patch area equal to 21.5 ha, (middle panel) patch area equal to 14.4 ha, and (right panel) patch area equal to 2.5 ha.
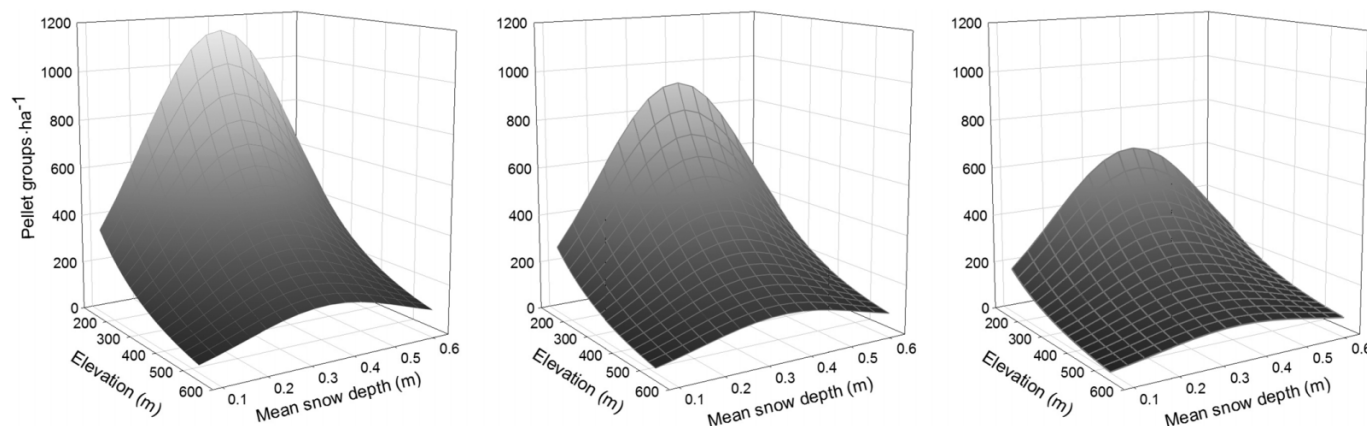
Messier 2000; Dussault et al. 2005). Forest management practices of the region have led to a study area that is dominated by second- and third-growth deciduous forests, which to varying degrees occupied much of the landscape surrounding these remnant patches of hemlock, and the negative influence of this homogenous cover type was evident, as well as implied, in our three greatest spatial extents. Large expanses of closed-canopy forests, those lacking in edge and therefore available browse, would be poor habitat for deer (Blouch 1984). Because the greater landscapes surrounding winter habitat likely serve as a source for wintering deer (Nelson and Mech 2006), we suggest that large expanses of deciduous cover in the landscapes surrounding the patch of interest may be the primary constraint to use of what might otherwise be high-quality winter habitat, and thus supporting the hierarchical scale of limiting factors proposed by Rettie and Messier (2000).

This influence of patch isolation, decreasing patch occupancy with increasing isolation, has been a tenet of landscape ecology for decades, where access to high-quality habitat has been shown to be impeded by a matrix of less than hospitable cover (cf. Ricketts 2001; Bradford et al. 2003; Bender and Fahrig 2005). Our results indicate a negative response to an increase in patch size of contiguous deciduous cover in the greater landscape, and we suggest that hemlock habitat embedded in a landscape of mature hardwood cover may be effectively isolated from use by wintering deer, especially in areas of higher snow depth. The composition of the matrix does, to a greater or lesser degree, influence patch occupancy (Gustafson and Gardner 1996; Ricketts 2001; Bradford et al. 2003; Bender and Fahrig 2005), and the probability of occupying a patch depends, in part, on the ability of a species to detect it (Olden et al. 2004). Although vast areas of mature hardwood forest type would be poor habitat for deer during any season (Millington et al. 2010), snow conditions have the potential to exacerbate this relationship. Snow cover has the potential to modify and even diminish the availability of forage (Turner et al. 1997; Nordengren et al. 2003), while simultaneously increasing the energetic cost to movement (Parker et al. 1984; Fancy and White 1985). Because snow accumulation under hardwood canopies has been shown to

be significantly greater than that of adjacent conifer patches (Kirchhoff and Schoen 1987), large patches of deciduous cover type may effectively limit the detection of or accessibility to high-quality winter habitat.

Across years, mean winter snow depth and elevation were important predictors of patch use at all spatial scales. Our results are consistent with research suggesting that at snow depths of 30–40 cm deer begin to or have already moved into winter habitat (Drolet 1976; Nelson and Mech 1981; Tierson et al. 1985; Sabine et al. 2002). In response to changes in snow depth, Morrison et al. (2003) found that during periods of low snow, white-tailed deer in New Brunswick spent more time in close proximity to browse on their wintering grounds. Conversely, at higher snow depths >0.5 m, deer were associated with areas of better cover. Our multiyear models suggest that deer yarding intensity, as predicted by pellet group counts, increases with increasing mean seasonal snow depth, and relative deer use peaks as mean snow depth approaches 0.4 m (Fig. 3). However, at snow depths beyond 0.4 m, we saw an inverse in this relationship, suggesting that fewer deer are found in the areas of highest snow depth. Additionally, our annual models suggest that at a lower mean annual snow depth, deer were more closely associated with the availability of within-patch forage. In our highest snow-depth winter (2007–2008: 0.43 m mean snow depth), more hemlock patches were utilized by wintering deer than in lower snow-depth years (Fig. 2), and our best models of patch use did not included forage availability.

We found no relationship between elevation and snow. Minor increases in elevation along the Lake Superior shoreline often lead to a gain in winter precipitation and a resultant snow shadow in areas adjacent to the lake (Stottlemyer and Toczydlowski 1991). Across the study area, a mixture of lake-effect and regional snowfall trends may be masking a more localized relationship between snowfall and elevation found in close proximity to Lake Superior.

In contrast to landscape heterogeneity, deer use decreased with an increase in heterogeneity in mean annual snow depth. This was evident both within and between years (Fig. 2). The decision to leave a patch is often based on the quality and availability of forage versus the cost of moving to a new

patch (Senft et al. 1987). Snow depth and density have been shown to impede ungulate foraging and movement (Parker et al. 1984), therefore leading to an increased cost to movement in higher snow-depth winters. Although hemlock was historically a common browse species of deer during winter (Dahlberg and Guettinger 1956), overbrowsing by deer and other limits to hemlock regeneration and recruitment across the region have led to hemlock patches devoid of available understory browse (cf. Anderson and Loucks 1979; Frelich and Lorimer 1985; Mladenoff and Stearns 1993; Rooney et al. 2000; Witt and Webster 2010). Deer must, therefore, find a balance in the trade-off between winter cover and browse acquisition. Although our study did not directly measure deer density or time spent in hemlock patches, it was clear that the intensity of winter yarding was lower in low snow and highly variable snow years (Fig. 2). As hemlock patches across the region provide little available browse, our data are congruent with the findings of Morrison et al. (2003) that deer will use areas of better forage during periods of lower snow depth. Thus, yearly heterogeneity in snow depth, as well as lower snow years, may allow the food–cover trade-off to be weighted more toward browse acquisition than in higher snow years.

Processes, and therefore behaviors, underlying habitat selection are dynamic, and among ungulate behaviors, site fidelity and predator avoidance are some of the additional factors that have been shown to have an influence on ungulate winter habitat selection (Nelson 1998; Van Deelen et al. 1998; Rettie and Messier 2000; Creel et al. 2005; Nelson and Mech 2006). After a 30-year absence, the Upper Peninsula of Michigan has experienced a recent recolonization by grey wolves (*Canis lupus* L., 1758) and as wolf densities of the region are highly correlated with deer densities (Potvin et al. 2005), this has likely led to shifts in deer winter habitat use. Although it is increasingly common to assess the influence of predation risk on habitat selection in ungulates, such assessments are rare for white-tailed deer living in mixed forests. In the one such assessment of which we are aware, deer did not appear to alter their habitat selection in direct response to predation risk at any spatial scale (Kittle et al. 2008). Instead, these deer managed predation risk by modifying habitat selection with respect to snow conditions. Knowing more about how deer in this study manage predation risk, either directly or indirectly, would undoubtedly reveal a more complex picture. However, it seems unlikely that a more complex picture would not also include the major conclusion of this analysis, which is that habitat selection by deer is influenced by snow at local scales and by composition and the configuration of the landscape at greater spatial scales. Further research should explore how land-use practices in close proximity to winter habitat, especially those practices that may provide additional forage, influence predation risk, patch fidelity, and the intensity of patch use.

Management implications

Our research suggests that, although it is clear that the hemlock patch itself is an important resource for wintering deer, the trade-off between risk and reward at the coarse scale of the greater landscapes may also be an important factor influencing use of these remnant patches of habitat. Management decisions made regarding specific patches would,

therefore, likely be ineffective unless the greater landscape was taken into consideration. For example, habitat modifications that lead to increased heterogeneity in the greater landscapes surrounding hemlock patches have the potential to lead to increased concentrations of wintering deer, thereby increasing within-patch browse pressure. In contrast, modifications made within or proximate to the patch of interest may have little influence over winter deer use if the patch remains isolated in a seemingly homogenous landscape. Consequently, our results suggest that interactions between deer migratory behavior, interannual variation in winter severity, and landscape context might provide spatial and temporal refugia for hemlock regeneration; a better understanding of which could aide conservation and restoration.

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