Forest cover, snow conditions, and black-tailed deer sinking depths

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Received October 19, 1989

BUNNELL, F. L., HOVEY, F. W., MCNAY, R. S., and PARKER, K. L. 1990. Forest cover, snow conditions, and black-tailed deer sinking depths. Can. J. Zool. **68**: 2403–2408.

Sinking depths of black-tailed deer (*Odocoileus hemionus columbianus*) and associated snow characteristics were recorded in old-growth, second-growth, and recently clearcut forests. Erratic deer movement in a 20-year-old stand prohibited measurements of deer sinking depth there, but a surrogate measure (human sinking depth) and associated snow characteristics were recorded. Both daily weather conditions and forest cover influenced deer sinking depths and associated snow conditions ($p < 0.001$). The two oldest stands had more shallow snowpacks with denser snow in the upper layers and greater mean hardness values than did the clearcut. As a result, mean deer sinking depths were lower in those stands. For all but 1 day ($n = 9$), forested habitats showed consistent rankings relative to the potential for deer movement: clearcut (worst) < 20-year-old < old growth and 80-year-old (about equal and best).

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La profondeur d'enfoncement des Cerfs mulets (*Odocoileus hemionus columbianus*) dans la neige et les caractéristiques de la neige ont été enregistrées dans des forêts anciennes, des forêts récentes et des zones de coupe à blanc. Les déplacements irréguliers des cerfs dans une forêt de 20 ans n'ont pas permis de mesurer leur profondeur d'enfoncement dans ce milieu, mais une mesure de remplacement (profondeur d'enfoncement d'un homme) et les caractéristiques de la neige y ont été enregistrées. Les conditions climatiques chaque jour et la couverture offerte par la forêt influençaient la profondeur d'enfoncement et les caractéristiques de la neige ($p < 0,001$). Les deux forêts les plus anciennes avaient des amas de neige moins épais, plus denses dans les couches supérieures, avec des valeurs moyennes de dureté plus grandes que les amas de neige des zones coupées. Par conséquent, les profondeurs d'enfoncement moyennes étaient plus faibles dans les forêts plus âgées. À l'exception d'une seule journée ($n = 9$), les forêts occupaient toujours le même rang quant à leurs propriétés de faciliter les déplacements des cerfs : zones de coupe à blanc (au bas de l'échelle) < forêts de 20 ans < forêts anciennes et forêts de 80 ans (environ égales et au haut de l'échelle).

[Traduit par la revue]

Introduction

In Washington, British Columbia, and Alaska snow influences both distribution and survival of black-tailed deer, *Odocoileus hemionus columbianus* (Klein and Olson 1960; Brown 1961; Bunnell *et al.* 1978; Wallmo and Schoen 1980; Jones and Bunnell 1984). One influence of snow is to hinder deer movement, thus increasing energy costs and limiting use of some habitats (Bunnell and Jones 1984; Parker *et al.* 1984). Under conditions of heavy snowfall, old-growth forests are considered the best black-tailed deer habitat (Bunnell and Eastman 1976; Schoen *et al.* 1981; Bunnell and Jones 1984), but some workers have suggested that appropriate silvicultural prescriptions could create favourable winter range in managed, second-growth stands (Harestad *et al.* 1982; Bunnell 1985; Nyberg *et al.* 1986). Many studies have addressed forest–snow or snow–ungulate relations (reviews of Shank and Bunnell 1982*a*, 1982*b*; Bunnell *et al.* 1985); only Bunnell *et al.* (1990) sampled deer movement under controlled conditions (same animal compared across different forest stands under the same weather conditions). Hanley and Rose (1987) and Kirchhoff and Schoen (1987) described forest influences on snow attributes considered important to black-tailed deer but did not measure sinking depths.

Bunnell *et al.* (1990) reported the influences of different snow attributes, regardless of forest cover, on deer sinking depth. Here we evaluate the relative suitability of different kinds of forest cover for black-tailed deer movement through snow.

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Study areas and methods

Study areas

Data were collected on 9 days selected during the period 22 January to 13 April 1984 to encompass different snow characteristics under stable weather conditions, i.e., minimal wind and precipitation, and minor changes in temperature and solar radiation within each day. The days were representative of the range of snow conditions but may not represent the frequency with which particular kinds of snow occur. Each day sampling occurred in four habitats located on southern slopes (elevation: 950–970 m) of the subalpine Mountain Hemlock Zone (sensu Krajina 1965) in Mount Seymour Provincial Park, British Columbia. Dominant tree species were mountain hemlock (*Tsuga mertensiana*), Pacific silver fir (*Abies amabilis*), and yellow cedar (*Chamaecyparis nootkatensis*). The habitats were (*i*) a 200-year-old stand averaging 60% crown closure as measured by moosehorn (Robinson 1947), (*ii*) an 80-year-old, second-growth stand with 90% crown closure, (*iii*) a 20-year-old stand with 36% crown closure, and (*iv*) a clearcut area with no overstory cover. Deer sinking depths and associated snow attributes were measured on 5 days of markedly different snow conditions in three habitats ($n = 630$). Extreme variability in snow conditions in the 20-year-old stand (air pockets around shrubs and small trees) influenced the behaviour and gait of the tame deer; the deer either refused to move or bounded erratically. Trials using deer were abandoned in that habitat. Human sinking depths and associated snow attributes include four habitats and 4 additional days ($n = 850$).

Sinking depths and snow characteristics

Sinking depths were determined for captive black-tailed deer by the methods of Bunnell *et al.* (1990). With the exception of 1 day during which weather conditions changed quickly and snow measurements were abandoned in two habitats, sampling with the deer occurred over a 6- to 8-h period in six plots in old- and second-growth stands and three plots in a clearcut area. All plots were located on relatively flat terrain where the deer could take at least 10 steps without altering its gait.

In each plot, sinking depths of 10 individual deer tracks were measured to the nearest centimetre as the vertical distance from snow surface to the tip of the hoof track. Within as close a proximity as possible to each track, hardness (g/cm^2) of any upper crust and minimum load (g/cm^2) necessary to reach the same sinking depth as the deer were determined using the snow penetration gauge (SPG) of Hepburn (1978). Human booted-foot sinking depth was recorded near each deer track. Density (g/cm^3) was estimated with a Stevenson's snow sampler next to 5 of the 10 deer tracks. Snow depth was recorded at each deer sinking depth, hardness measurement, and density tube reading.

Additional data on snow characteristics and human sinking depths were collected using systematic sampling in the same habitats, including 20-year-old forest. Techniques were the same. Each transect was sampled across the slope and parallel to contours. Plots were located 2.5 m apart on transects. All habitats contained 60 plots except clearcut which contained 40.

Analysis

Potential differences in sinking depth, density, and hardness among plots, habitats, and days were evaluated by analysis of variance. Because all distributions but one were normal (Pearson's goodness-of-fit test), tests for homogeneity of variance used Bartlett's χ^2 (Sokal and Rohlf 1981, p. 404). Variance was heteroscedastic and no effective transforms were found so ANOVAS were repeated using standard normal scores (e.g., Conover 1971, p. 291; Conover and Iman 1981). Levels of significance of the F-ratio remained unchanged, indicating that differences were so pronounced that analysis of untransformed data was informative. Except for Scheffé's tests of differences between habitats or other classes, the level of significance was ≤ 0.05. Scheffé's test is conservative (Jones 1984) and the level chosen for significance was ≤ 0.10. The likelihood of different distributions in snow characteristics among habitats regardless of day effects (evident in ANOVA) was evaluated using untransformed data and Kolmogorov–Smirnov tests (Conover 1971, pp. 309–314). Tests of the independence of proportions of specific variables followed Hicks (1982, pp. 31 and 32).

Results

Forest cover and snow

All measurements (deer sinking depth, hardness, and density) exhibited significant differences associated with plot, day, and habitat ($p < 0.002$, Table 1). Plots were destructively sampled and treated as a random effect nested within the fixed effects of day and habitat. Day was treated as a fixed effect because days were selected to encompass specific, stable weather conditions. The significant plot effect reflects the large variability in snow conditions. Interaction between day and habitat was significant for all variables, except hardness measured as minimum load to reach deer sinking depth ($p > 0.05$), and was highly significant for deer sinking depth ($p < 0.001$, Table 1). The interaction between day and habitat was largely attributable to day 3 when greater crusting and density in the clearcut reduced sinking depths there (Fig. 1). If plot is treated as a fixed effect all F-ratios of the model are highly significant ($p < 0.001$), which emphasizes the variability in snow conditions.

There were pronounced differences among habitats. Older stands had significantly denser snow in the upper layers and greater mean hardness values than did the clearcut (Table 2). As a result, mean deer sinking depths were significantly lower in those stands.

Forest cover and deer movement

Mean sinking depths permit broad comparisons but do not directly express potential differences in energy costs of movement. The influence of sinking depth on energy costs of deer in

TABLE 1. Mixed-model analysis of variance for a nested-factorial experiment on deer sinking depth, snow hardness, and snow density in entire pack or to 48 cm depth (data are from Mount Seymour, B.C., 1984)

Source	SS	df	MS	F-ratio	P
Deer sinking depth					
$Plot_{i(jk)}$	2 234.8	51	43.8	2.93	≤ 0.0001
Day_j[a]	26 192.0	3	8730.5	199.24	≤ 0.0001
$Habitat_k$[b]	7 028.1	2	3514.1	80.19	≤ 0.0001
Day × $Habitat_{jk}$	8 194.5	6	1365.7	31.17	≤ 0.0001
$Residual_{m(ijk)}$	8 492.6	567	15.0		
Total	51 690.0	629			
Hardness to deer sinking depth					
$Plot_{i(jk)}$	8.4×10^7	51	1.6×10^6	1.76	≤ 0.0012
Day_j	2.5×10^8	3	8.4×10^7	50.80	≤ 0.0001
$Habitat_k$	2.7×10^7	2	1.3×10^7	8.10	≤ 0.0001
Day × $Habitat_{jk}$	2.2×10^7	6	3.6×10^6	2.20	≤ 0.0583
$Residual_{m(ijk)}$	5.3×10^8	567	9.3×10^5		
Total	9.2×10^8	629			
Density of snowpack					
$Plot_{i(jk)}$	0.392	51	0.008	3.12	≤ 0.0001
Day_j	0.184	3	0.061	7.97	≤ 0.0001
$Habitat_k$	0.107	2	0.053	6.95	≤ 0.0021
Day × $Habitat_{jk}$	0.160	6	0.027	3.46	≤ 0.0061
$Residual_{m(ijk)}$	0.616	250	0.002		
Total	1.469	312			
Density to 48 cm[c]					
$Plot_{i(jk)}$	0.395	46	0.008	2.80	≤ 0.0001
Day_j	0.437	3	0.146	16.96	≤ 0.0001
$Habitat_k$	0.500	2	0.250	29.15	≤ 0.0001
Day × $Habitat_{jk}$	0.119	5	0.024	2.78	≤ 0.0283
$Residual_{m(ijk)}$	0.505	165	0.003		
Total	2.246	221			

[a] On 1 day snow conditions changed before sampling could be completed in all three habitats; only 4 days included in the ANOVA.
[b] Only the three habitats in which deer sinking depths were measured are treated.
[c] Includes all samples of snow density ≤ 48 cm depth.

snow is nonlinear and further modified by density (Parker *et al.* 1984). Furthermore, the distribution of hardness measurements was nonnormal ($\chi^2_7 = 209.75$, $p < 0.001$) and the strong habitat–day interaction for deer sinking depth (Table 1) suggests that direct comparisons of means among habitats are potentially misleading. Data are therefore presented as cumulative frequency distributions (Fig. 2). For example, the proportion of sinking depths in the region of rapid increase in movement costs (>40% brisket height, Parker *et al.* 1984) was 50% in clearcuts, 25% in old growth, and only 8% in 80-year-old second growth (Fig. 2). Proportions of hardness measurements less than 512 g/cm^2 (foot loading of deer standing on two feet, Bunnell *et al.* 1989) were about 20% in second growth, 25% in old growth, and 55% in the clearcut (Fig. 2). The greater proportions of low hardness and of low density values in the clearcut each contributed to the greater sinking depths there.

These comparisons are more useful if the rankings of habitats show a consistent tendency regardless of the day effect evident in ANOVA (Table 1). Kolmogorov–Smirnov tests combined days to evaluate general habitat effects. Because human sinking depth and deer sinking depth were highly correlated ($r = 0.81$) and responded similarly to snow conditions (Bunnell *et al.* 1990), analyses were extended to cases for which only human

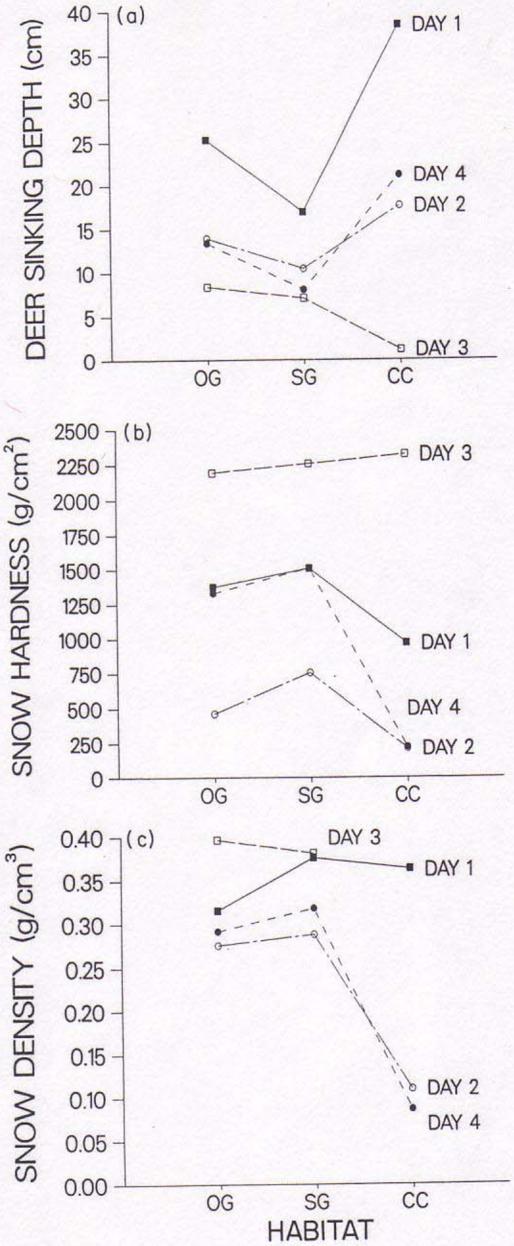

FIG. 1. Mean values by day and habitat for (*a*) deer sinking depths, (*b*) snow hardness to deer sinking depths, and (*c*) density of the upper 48 cm of snowpack (<48 cm when pack <48 cm deep). Interactions are apparent between day and habitat (OG = old growth, SG = second growth, CC = clearcut). The interaction for hardness is not significant ($p = 0.058$, Table 1).

sinking depths were measured. Each sampling design was treated separately, providing independent evaluations.

The rankings among broad habitat types for deer sinking depths and two sample designs of human sinking depth (plots with deer, transects without deer) were consistent and showed significant differences among habitats ($p < 0.001$). With one exception, the analyses indicated that the relative ranking of habitat types for sinking depth, from worse (deepest) to best (shallowest), was clearcut < 20-year-old < old growth < 80-year-old. The exception was a reduction of sinking depths in the clearcut on day 3 when weather conditions produced hard surface crusts (Fig. 1).

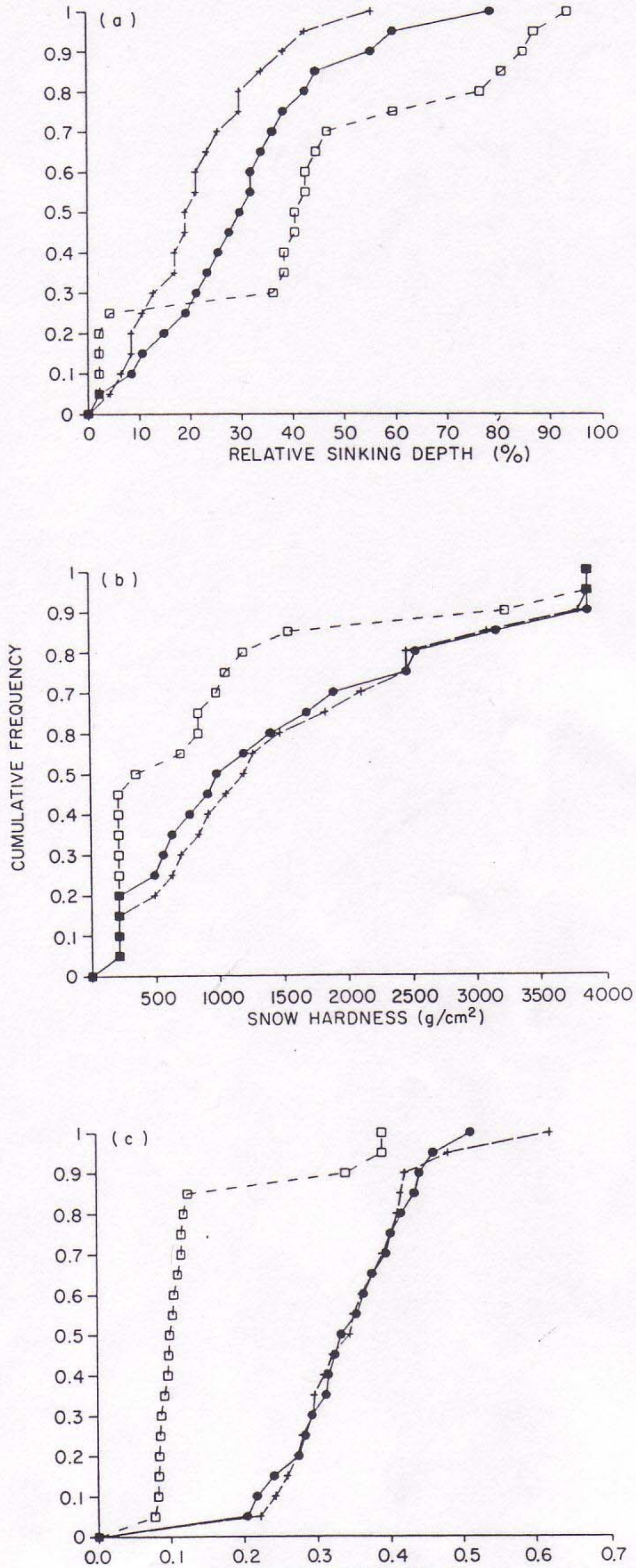

FIG. 2. Cumulative frequency distributions of relative sinking depths, snow hardness, and density in old-growth (●), second-growth (+), and clearcut stands (□).

TABLE 2. Mean values of snow characteristics and deer sinking depths in three forested habitats on Mount Seymour, B.C., 1984

Variable	N	Habitat: Clearcut	Habitat: Old growth	Habitat: 80-year-old
Density, ≤48 cm (g/cm³)	222	0.16	0.33*a*	0.34*a*
Density, entire pack (g/cm³)	343	0.40*b*	0.37*bc*	0.35*c*
Hardness (g/cm²)	630	991.80	1389.70*d*	1569.40*d*
Snow depth (cm)	258	137.80	57.60	32.40
Deer sinking depth (cm)	630	19.00	14.70	10.00

NOTE: For each variable, values followed by the same letter do not differ significantly using Scheffé's test, $p = 0.10$.

TABLE 3. Differences in proportions of habitat values critical to deer movement in snow among forest habitats on Mount Seymour, B.C., 1984

Variable	N	Relative rank: Worst						Best
Deer sinking depth >40% brisket height	630	Clearcut (0.58)[a]	<0.001[b]		Old growth (0.24)		<0.001	80-year-old (0.09)
Density upper 48 cm, >0.4 g/cm³	222	Clearcut (0.0)	<0.01		80-year-old (0.26)		>0.9	Old growth (0.27)
Density upper 48 cm, <0.15 g/cm³	222	Clearcut (0.89)	<0.01		Old growth (0.0)		>0.9	80-year-old (0.0)
Hardness, <257 g/cm²	630	Clearcut (0.48)	>0.10		Old growth (0.23)		>0.10	80-year-old (0.19)
Hardness (<257 g/cm²)[c]	220	Clearcut (0.36)	<0.10	20-year-old (0.20)	>0.9	Old growth (0.19)	>0.05	80-year-old (0.13)
Hardness (>2048 g/cm²)	630	Clearcut (0.13)	<0.05		Old growth (0.28)		>0.8	80-year-old (0.32)
Hardness (>2048 g/cm²)[c]	220	Clearcut (0.09)	<0.9	20-year-old (0.10)	<0.01	Old growth (0.26)	>0.05	80-year-old (0.32)

[a]Specific proportions are given in parentheses.
[b]Test of difference in proportions between adjacent elements in a row; probability of no difference.
[c]Includes hardness measurements in 20-year-old stand where deer sinking depths not measured.

Because of the nonlinear relation between energy costs and sinking depth, we also evaluated potential differences in proportions of values which may be critical to deer among habitats. Critical regions included sinking depths >40% brisket height (Parker *et al.* 1989) and snow densities <0.15 g/cm³ (unfavourable) or >0.40 g/cm³ (favourable, Bunnell *et al.* 1990). Critical values for hardness were <256 g/cm² (no supporting crust) and >2048 g/cm² where sinking depths were significantly lower (Bunnell *et al.* 1990). When all data were combined, the clearcut was consistently worst in terms of deer movement, and 80-year-old second growth was most often best (Table 3). Usually there was no significant difference between older second growth and old growth.

Discussion

The estimate of crown closure used was mean crown completeness (MCC, sensu Bunnell *et al.* 1985, p. 181). Although Kirchhoff and Schoen (1987) found MCC less well correlated with snow deposition than were mean tree height and net inventory volume, MCC appears to be a useful stand measurement for characterizing winter ranges. Among the 15 ways of characterizing forest canopies they compared, Hanley and Rose (1987) and McNay *et al.* (1988) found MCC to be the best single variable predicting snow interception. Vales and Bunnell (1988) found MCC to be highly predictive of below canopy irradiance, thus forage potential.

Mean snow depths across the four habitats decreased linearly with MCC ($r^2 = 0.87$, $p < 0.05$), consistent with the model of Harestad and Bunnell (1981). Snow densities in the upper 48 cm were about twice as high under the two older canopies as in the clearcut; densities of the entire snowpack differed little (Table 2). Most workers measure the entire pack and report little difference with changing forest cover, including open areas (Shank and Bunnell 1982*b*; Hanley and Rose 1987). We measured the upper 48 cm separately, because 48 cm represented brisket height beyond which the deer could not sink. Bunnell and Jones (1984) suggested that forest cover would ameliorate snow conditions affecting deer movement by reducing depth and increasing density. Frequent rain-on-snow events of coastal forests were expected to increase snow densities under canopy through drip from the canopy (Bunnell *et al.* 1985). Our observations in the upper 48 cm support that expectation.

Hardness levels under older forest canopies also were greater than in clearcuts (Table 2). These observations are contrary to those from relatively dry forests (e.g., Kelsall and Prescott 1971; Peterson and Allen 1974). They are consistent with the predictions of Bunnell *et al.* (1985) that in wet coastal forests wind-induced crusting (more evident in clearcuts) would be less pronounced than crusting resulting from freeze–thaw cycles or rain-on-snow events resulting in drip and sloughing from the overstory. Pronounced crusting in the clearcut occurred on only 1 day (Fig. 1). Large variability in hardness also has been documented by others (e.g., Pruitt 1959, 1979; Kelsall and Prescott 1971; Eastman 1978).

The ranking of habitats (Table 3) reflects only suitability for movement. When provision of rooted forage and arboreal lichen is considered the relative value of old growth increases (Bunnell and Jones 1984; Bunnell 1985). There are three features of the data that could produce misleading rankings. First, although the samples include 9 days, the days were selected to encompass the range of potential snow conditions and not to estimate the most frequent snow conditions during a winter. The reversal in ranking that occurred on day 3 (Fig. 1*a*), however, appears to be an uncommon and ephemeral event in coastal British Columbia (Jones 1974). Second, the estimate of 0.4 g/cm^3 as the lower bound for densities favourable to moving deer may be too low. The present data (Fig. 2), however, indicate that the rankings among habitats would remain unchanged if a higher density threshold were chosen. Third, by using captive deer in selected habitats no opportunity for deer to choose the most suitable conditions for movement is permitted. Some workers (e.g., Telfer and Kelsall 1984) have argued that selection of movement routes from among different snow conditions is an important adaptive trait. We abandoned attempts to sample areas used and not used by deer in selected habitats when we documented fine-scale variability (Bunnell *et al.* 1990). We do not know if the deer would have moved through the 20-year-old stand if allowed to make its own choice. Failure to document selection of routes within the other three habitats does not alter their ranking of potential ease of movement.

Of the limitations noted, only the first is likely to modify rankings of the three habitats the deer used, and then under uncommon weather conditions. The significant differences in snow depth (Table 2) follow the ranking predicted on the basis of canopy closure (Harestad and Bunnell 1981; Bunnell *et al.* 1985). Differences in snow density and hardness, which also affect sinking depth, had not been assessed previously for western coastal forests. The rankings indicate that dense second-growth stands can provide favourable conditions for locomotion. This finding may explain the winter occurrence of deer in second growth (Bunnell 1979; McNay and Doyle 1987; Kremsater 1989), although old growth is considered highly preferred (Jones 1974; Schoen *et al.* 1981).

The most favourable stand for deer movement (80-year-old second growth) had a canopy closure of 90%, which permits only small amounts of rooted forage (Bunnell and Jones 1984). That observation supports suggestions that silvicultural prescriptions to create deer winter range in managed stands will require a mosaic of stand treatments (Bunnell and Eastman 1976; Bunnell 1985). Nyberg *et al.* (1986) offered tentative silvicultural prescriptions for creating winter range in managed stands. These data indicate that dense second-growth stands will provide suitable conditions for movement, but that untreated second-growth stands provide poor conditions at least until 20 years of age (Table 3). Some portion of the stand with lower MCC would be necessary to provide forage.

Acknowledgments

We thank R. D. Davies, L. L. Kremsater, R. K. McCann, and J. B. Nyberg for reviewing the manuscript. P. C. Smith provided the penetrometer. Our research was supported by the Science Council of British Columbia and the Natural Sciences and Engineering Research Council of Canada.

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