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Forest Habitats and the Nutritional Ecology of Sitka Black-Tailed Deer: A Research Synthesis With Implications for Forest Management

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Abstract

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Research on forest habitats and the nutritional ecology of Sitka black-tailed deer conducted during 1981 through 1986 is reviewed and synthesized. The research approach was based on the assumption that foraging efficiency is the best single measure of habitat quality for an individual deer. Overstory-understory relations and the influence of forest overstory on snow depth and density, forage availability, and forage quality were studied in the western hemlock-Sitka spruce forests of southeastern Alaska. The effects of forest management were analyzed in terms of their consequences of changing the historic disturbance regime of old-growth forests from one of high-frequency, low-magnitude disturbance to the low-frequency, high-magnitude disturbance regime of even-aged forests. Old-growth and even-aged forests differ greatly in their production of forage, protein digestibility of sun- and shade-grown leaves, and relative carrying capacities for deer. Forest overstories reduce snow depths significantly, but only at high crown closures (>95 percent). Analyses of species composition and quality of the diet of black-tailed deer and nutritional quality of forages indicated digestible energy and digestible protein are probably the potentially greatest nutritional limiting factors for deer in Alaska. Digestible protein probably is not limiting in shaded habitats but may be the greatest limitation to deer productivity and carrying capacity in clearcuts during summer. Digestible energy is probably the most limiting factor in forests during summer and all habitats during winter. Modeling of foraging energetics indicated snow, even at low depths, is a critical factor affecting foraging efficiency and carrying capacity of habitats. Its greatest effect is on reducing energy intake by changing forage availability and diet composition rather than by increasing energy costs of locomotion. Foraging efficiency and carrying capacity are shown to be related but very different concepts: for black-tailed deer, forage biomass is a relatively minor factor affecting foraging efficiency but a major factor affecting carrying capacity. It is suggested that habitats be evaluated primarily on the basis of nutritionally based estimates of carrying capacity and that greater emphasis be placed on summer and spring range than is currently the practice. Retention of old-growth forests for winter range during periods of snow will remain an important feature of habitat management for deer while techniques for increasing the carrying capacity of even-aged stands are sought.

Keywords: Deer, black-tailed deer, Sitka black-tailed deer, *Odocoileus hemionus*, wildlife, habitats, forest management, Alaska, southeastern Alaska, nutrition, ecology.

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Introduction

In 1981, a 5-year problem analysis was written, initiating USDA Forest Service research on the nutritional ecology of Sitka black-tailed deer in Alaska. (See "Common and Scientific Names" for scientific names of animals and plants.) The literature review of that problem analysis was later published (Hanley 1984b); it provides a summary of Alaska deer research through 1980. The purpose of this report is to summarize and synthesize our research conducted from 1981 through 1986. Our emphasis is on a practical interpretation of the findings and a development of the major implications for forest management.

The fundamental assumption of the research approach was that foraging efficiency provides the best single measure of habitat quality for an individual deer. Foraging efficiency is the difference between energy intake and energy expenditure by a deer while searching for and consuming food. It is influenced by the quantity and quality of understory vegetation as food and the depth and density of snow as it affects the availability of vegetation and mobility of deer. Forest management affects deer by altering the overstory, which in turn affects understory production and snow interception, and, ultimately, foraging efficiency (fig. 1). As foraging efficiency increases, deer are able to accumulate more body reserves (or deplete them at a slower rate) and/or spend less time foraging. Reproductive performance and longevity increase with improved body condition. And the less time a deer must spend foraging, the more time it has for other activities, such as resting and staying alert for predators.

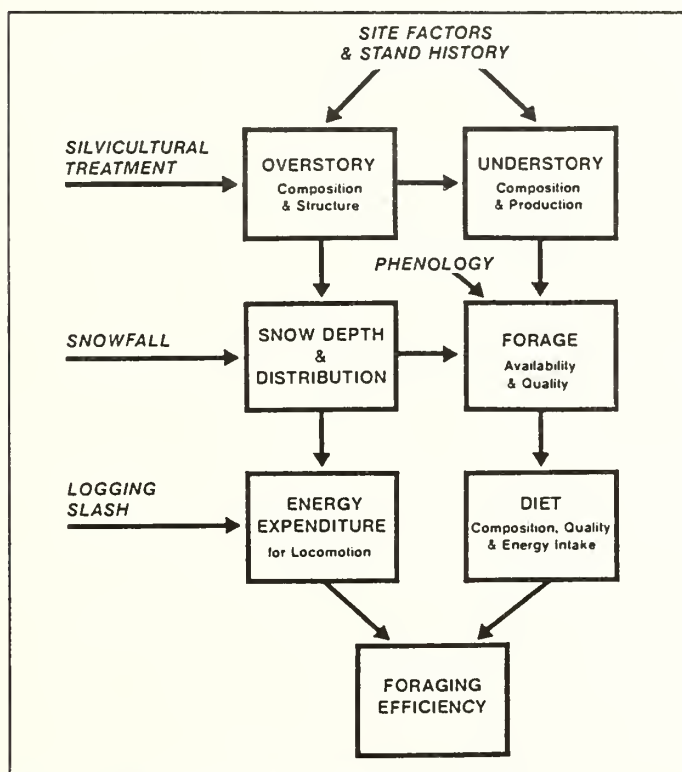


Figure 1—Interactions of factors determining foraging efficiency.

Foraging efficiency, therefore, provides an important theoretical basis for habitat selection and the well-being of individual deer. In turn, it is an important factor determining carrying capacities of habitats for populations of deer.

The research initiated in 1981 addressed a broad range of factors affecting foraging efficiency. It had six major components: (1) overstory-understory relations, (2) snow depth and density, (3) forage availability and quality, (4) diet composition and energy intake, (5) energy expenditure, and (6) foraging efficiency.

Overstory- Understory Relations¹

Old-Growth Forests

The low-elevation, old-growth forests of southeastern Alaska are characterized by western hemlock-Sitka spruce overstories; understories are dominated by Alaska blueberry and skunkcabbage. Flood plain communities are typically Sitka spruce overstories and devilscub-dominated understories. Muskegs, characterized by scattered shore pine, Alaska yellow-cedar, and western or mountain hemlock with Labrador tea- and sedge-dominated communities, are also common. Most logging, however, occurs within the hemlock-spruce forests with blueberry and skunkcabbage understories. These are the stands most potentially subject to intensive forest management.

In an analysis of 34 such stands on Admiralty and Prince of Wales islands, Brady (1986) classified the understories into two major groups on the basis of their species composition and production: 19 stands in an Alaska blueberry/bunchberry dogwood group and 15 stands in an Alaska blueberry/skunkcabbage group (table 1). Understories of both groups were comprised of the same species but differed in the relative abundance of each species along a gradient ranging from communities dominated strongly by blueberry to others dominated strongly by skunkcabbage (fig. 2). Soil drainage appeared to be the most important environmental factor determining understory species composition and was associated with overstory mass (timber volume) as well. Stands of the blueberry/bunchberry understory type were characterized by greater overstory mass (timber volume), lower understory production, and better soil drainage than were stands of the blueberry/skunkcabbage type. The two types did not differ in overstory species composition or canopy coverage. And although total

¹ In this report, "old-growth forest" refers to naturally occurring stands with the predominant disturbance regime characterized by gap-phase succession (that is, small but frequent disturbance events resulting in the periodic loss of individual trees or small groups of trees from the overstory, with resulting gaps in the overstory being filled by trees growing up from the forest floor rather than simply lateral extension of surrounding limbs). Dominant and codominant trees encompass a wide range of ages and are usually, though not necessarily, older than 200 years. "Even-aged forests" are stands where most of the dominant and codominant trees are about the same age and are still responding to the same disturbance event that initiated stand regeneration. Gaps that periodically form in the overstory from the loss of individual trees are filled by lateral expansion of limbs of surrounding trees. Even-aged stands are usually, though not necessarily, younger than 200 years. "Clearcuts" refers to even-aged stands resulting from clearcut logging and still young enough (usually less than 20-30 years) that the conifer canopy has not yet closed or reached its stage of maximum closure.

Table 1—Net production of vascular understory vegetation in 3 types of understory communities in old-growth stands on Admiralty Island and Prince of Wales Island^a

Species	Communities		
	Hemlock-spruce upland sites		Spruce riparian
	Blueberry/ bunchberry ^b	Blueberry/ skunkcabbage ^c	Devilsclub/ lady-fern ^d
Forbs and ferns:	<i>Kilograms per hectare</i>		
<i>Athyrium filix-femina</i>	4.3	34.5	336.2
<i>Blechnum spicant</i>	12.8	15.5	0
<i>Coptis asplenifolia</i>	4.5	5.2	8.0
<i>Cornus canadensis</i>	23.9	38.7	.3
<i>Dryopteris dilatata</i>	7.7	0	54.9
<i>Gymnocarpium dryopteris</i>	10.6	5.0	19.6
<i>Listera cordata</i>	.2	1.1	0
<i>Lysichiton americanum</i>	0	200.2	0
<i>Maianthemum dilatatum</i>	5.4	6.0	3.5
<i>Monesis uniflora</i>	6.1	5.2	0
<i>Rubus pedatus</i>	14.7	14.0	15.4
<i>Streptopus amplexifolius</i>	.2	.1	0
<i>Streptopus</i> spp.	.5	.3	1.1
<i>Tiarella trifoliata</i>	4.0	4.3	108.5
<i>Viola glabella</i>	.1	1.0	0
Shrubs:			
<i>Gaultheria shallon</i>	.3	4.9	0
<i>Menziesia ferruginea</i>	15.6	64.7	0
<i>Oplopanax horridum</i>	6.2	9.9	125.9
<i>Rubus spectabilis</i>	7.3	5.3	0
<i>Vaccinium alaskensis</i>	9.7	110.5	14.4
<i>Vaccinium parvifolium</i>	.4	.9	0
<i>Vaccinium</i> spp.	10.5	7.7	0
Conifer seedlings:			
<i>Picea sitchensis</i>	10.5	1.3	144.3
<i>Thuja plicata</i>	2.3	0	0
<i>Tsuga heterophylla</i>	26.2	28.6	0
Others:			
<i>Carex</i> spp.	0	1.6	0
<i>Lycopodium</i> spp.	.4	5.1	0

^a Adapted from Brady (1986).

^b 19 stands sampled.

^c 15 stands sampled.

^d 1 stand sampled.

understory production (current annual growth, kilograms per hectare) was significantly ($P < 0.05$) negatively correlated with overstory canopy coverage in the Admiralty Island data set, the relation was not statistically significant for the Prince of Wales data set or for the combined data from both islands (fig. 3). For the old-growth, hemlock-spruce forests of southeastern Alaska, predicting understory species composition or production from aerial photographs or other currently available methods of remote sensing and vegetation mapping appears unlikely.

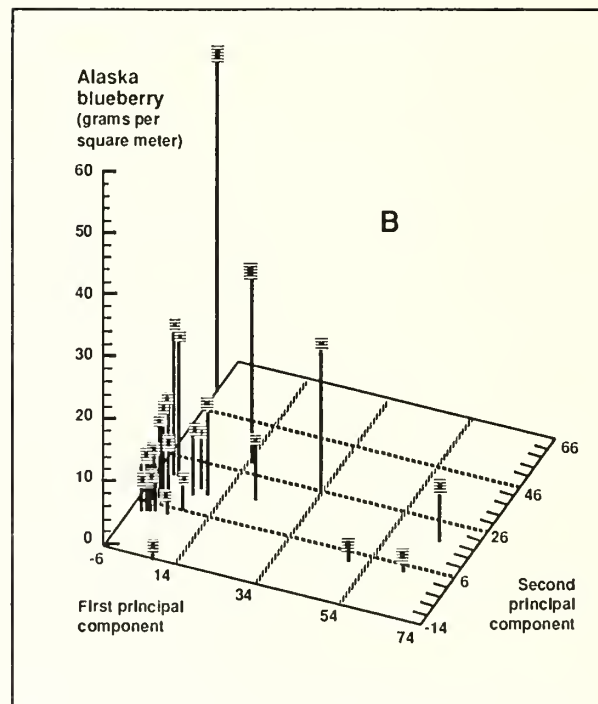
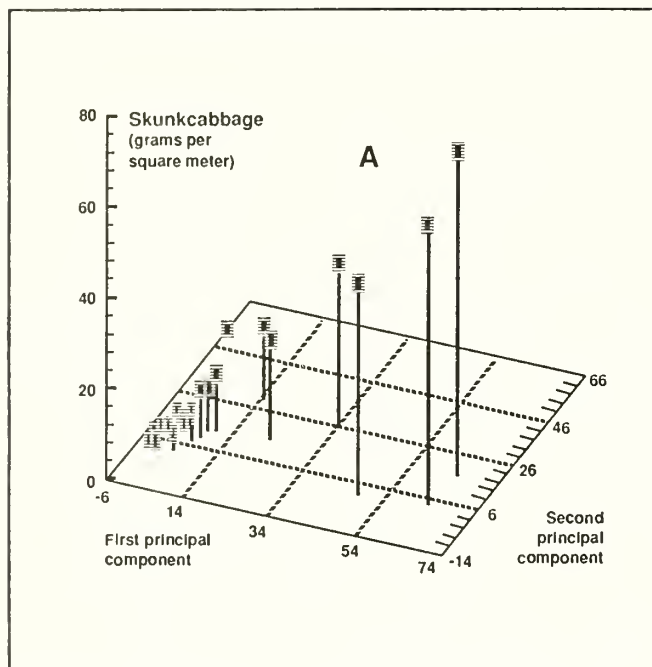


Figure 2—Net production of three major understory species in relation to the ordination of stands on the first and second principal components (adapted from Brady 1986): A. Skunkcabbage. B. Alaska blueberry. C. Lady fern.

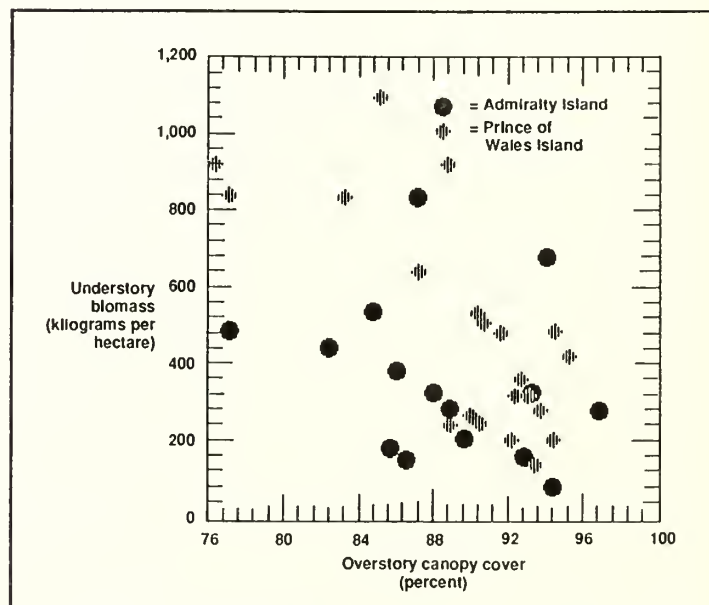
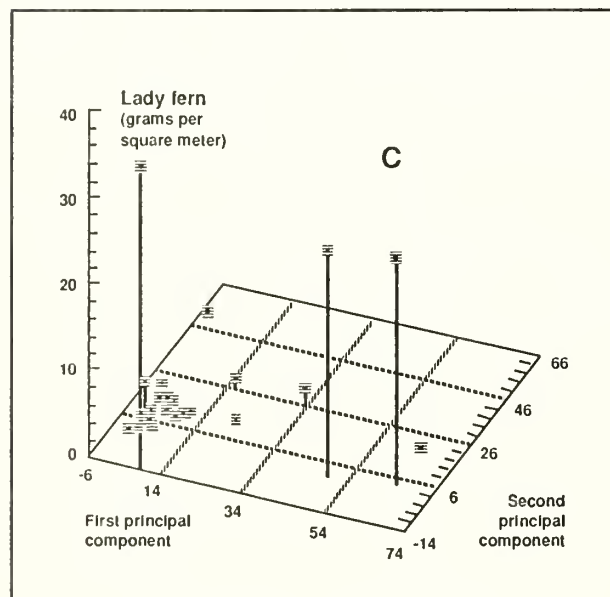


Figure 3—Plot of total net production of vascular understory species in old-growth stands on Admiralty and Prince of Wales Islands in relation to overstory canopy coverage (adapted from Brady 1986).

General patterns, however, are evident. For example, environmental factors related to open overstories (with low tree density and/or tree vigor) are associated with high levels of understory production. Thin, rocky soil and alluvial terraces often have the least dense overstories and, consequently, the most productive understories (Alaback 1984). But quantitative relations between environmental variables and understory species composition and production have, so far, proved very imprecise.

The lack of correlation between overstory characteristics and understory composition and productivity is in part related to stand history, particularly the disturbance regime of each stand (Alaback 1984, Brady and Hanley 1984). Species composition and biomass reflect not only the current environment but also the past environmental conditions. Understory responds to gaps in the overstory, but the response is not immediate, and time lags result. Understory species composition and biomass, buried seed banks and proximity to seed sources, as well as the disturbance regime influencing understory environment, all are important determinants of understory dynamics. Stands originating from windthrow, or subject to periodic windthrow, for example, usually are much more variable in understory than stands originating from logging (Alaback 1984). The historical aspect of stand development will always confound simple relations between overstory and understory. Overstory structure and understory species composition and biomass are dynamic, not static, properties of stands.

Even-Aged Stands

The successional sequence of understory development after logging of hemlock-spruce stands in southeastern Alaska has been described by Alaback (1982). In a broad sense, it is quite predictable, with large increases in understory production during the first 15-30 years, followed by a sharp decrease in production (to near-zero levels) as the conifer overstory closes and remains mostly closed for the next 120 or more years. But within this general pattern remains a substantial degree of variation (Alaback 1982, 1984). The understory of stands with high site index usually reaches greater peak biomass, becomes shaded out earlier, and reaches lower levels of biomass during the closed-canopy phase than does the understory of stands with low site index (Alaback 1984). The amount of understory within even-aged stands is mostly related to the distribution and abundance of gaps in the canopy. Alaback (1984) found that 75 percent of total shrub cover and 70 percent of total herb cover within even-aged stands occurred directly under canopy gaps, which suggests that silvicultural thinnings may offer a way of maintaining a productive understory through a rotation.

Although before-and-after studies of understory response to thinning have only recently been initiated, and a complete picture is not yet available, a preliminary study by Alaback and Tappeiner (1984) provides some insights into what may occur. Alaback and Tappeiner measured understory biomass in twenty-nine 0.4-ha even-aged stands that had been thinned 5 to 7 years earlier at spacings of 2.4 to 4.0 (light), 3.7 to 5.5 (medium), and 4.9 to 7.3 m (heavy) between trees. The stands ranged in age from 20 to 72 years old at the time they were measured and were scattered throughout southeastern Alaska as part of an experiment on the effects of stand density on tree growth and yield. Ten stands were 20 to 30 years old and were examples of what might be termed "precommercial" thinning. The other 19 stands were 39 to 72 years old and were examples of what might be called "commercial" thinning. All stands were a mixture of western hemlock and Sitka spruce.

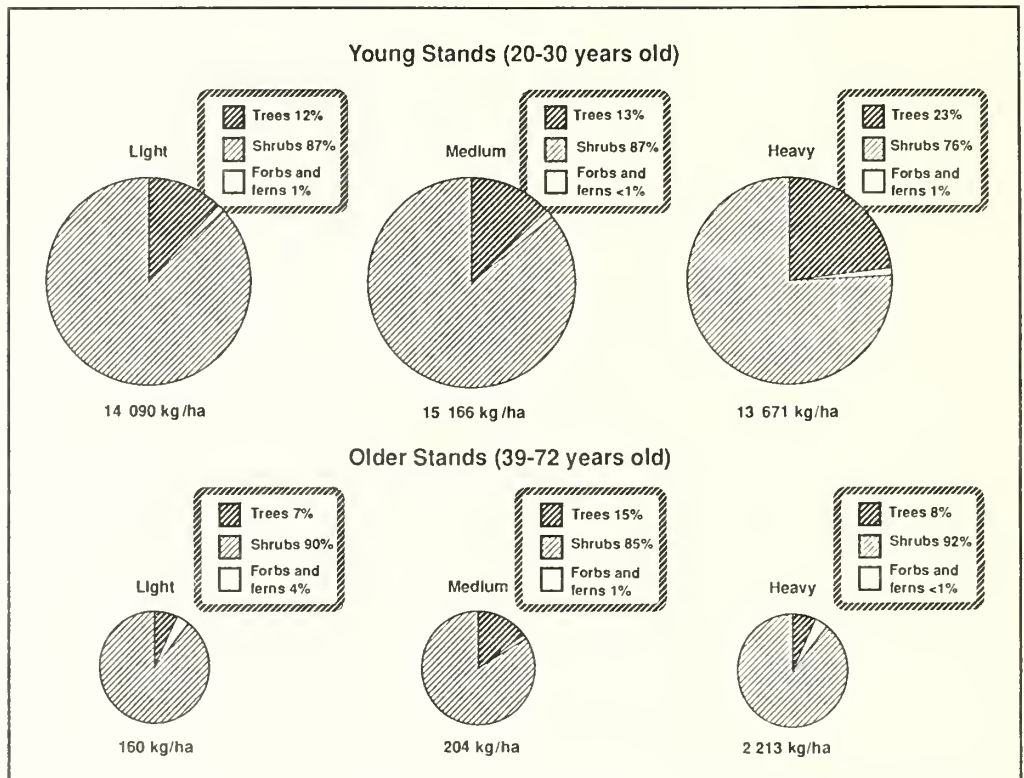


Figure 4—Vascular biomass of understory vegetation of hemlock-spruce stands 5 to 7 years after thinning at three levels of intensity (light, medium, heavy). Total understory biomass is indicated beneath each circle (data from Alaback and Tappeiner 1984).

Alaback and Tappeiner's results indicated a very high degree of variance between stands (that is, no significant differences in understory biomass with respect to tree spacing) in both young (20 to 30 years) and older (39 to 72 years) stands. Young stands, however, had 5 to 10 times the understory biomass of older stands (fig. 4). The proportions of biomass in shrubs, forbs, ferns, and trees remained relatively constant across stand ages and thinning intensities. Shrubs (primarily Alaska blueberry on upland sites and salmonberry on wetter sites) constituted about 76 to 92 percent of the total vascular biomass, and trees (primarily western hemlock seedlings) about 7 to 23 percent of the total. Forbs and ferns were consistently minor components of the understories after thinning. These results indicate three potentially important problems with thinning to maintain understory throughout a rotation. First, understory is slow to respond to thinning of older stands that have not been thinned before. Second, the understory that results from thinning is likely to be strongly dominated by two species and to consist almost entirely of woody shrubs and trees, rather than the more balanced distribution of shrubs, trees, forbs, and ferns typical of old-growth forests (compare with table 1). And third, as the stand matures, subsequent periodic thinnings will be necessary, and the understory is likely to become increasingly dominated by western hemlock to the eventual exclusion of even the shrubs. Maintaining a floristically diverse and productive understory through a rotation appears to be a more difficult problem than was first thought.

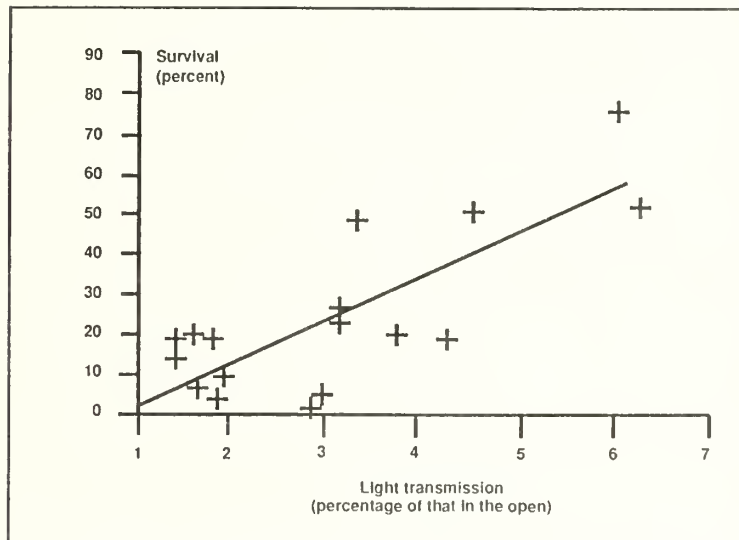


Figure 5—Relation between 3-year survival of Alaska blueberry seedlings (percentage of 1st-year germinants) and light transmission (percentage of that in the open) on the forest floor (from Tappeiner and Alaback 1986).

Autecology

The slow response of understory to thinning of older stands prompted investigations into the reproductive ecology of five common species: Alaska blueberry, bunchberry dogwood, trailing bramble, fernleaf goldthread, and foamflower. Tappeiner and Alaback (1986) compared seed production, germination, seedling establishment, and survival of these five species on various substrates of the forest floor in a 45-year-old, even-aged stand and an adjacent old-growth stand near Juneau. Their results indicated the greatest problem affecting the establishment and growth of understory vegetation lies in seedling survival, which was positively correlated with the availability of light (fig. 5). Differences in seed germination and seedling establishment were minor between the young and old stands, but seedling survival after 3 years was much less in the young stand than in the old. Apparently, seedlings readily become established in most forest habitats but experience very slow growth rates and low survival in the dark, cool understories of even-aged stands. The inherently slow growth rates of young seedlings rather than establishment appears to limit understory response to thinning of older, unthinned stands. Plants with well-developed root systems (the 20- to 30-year-old thinned stands, for example) are able to respond to thinning much more quickly than those developing from seed.

All of the species studied by Tappeiner and Alaback (1986) grew better in natural canopy openings (gaps) than under closed canopies. These species are well adapted to low-magnitude, high-frequency disturbance that creates gaps in the forest overstory. All propagate vegetatively by sprouting and sending out runners or rhizomes and reproduce sexually only under canopy gaps or in large openings (Tappeiner and Alaback 1986).

Snow Depth and Density

The influence of forest overstory on snow depth and density is important because snow affects the availability of food and energy costs of locomotion for deer. Most studies of forest influences on snowpacks have been conducted in areas of deep snow accumulation and have measured snow-water equivalent (depth times density). Few studies have been conducted in areas of shallow or transient snow, and few studies have reported results for depth and density separately. In southeastern Alaska, deer winter at low elevations in areas of transient snow. Energy expended by deer to move in snow is a function of both snow depth and density but not snow-water equivalent (Parker and others 1984).

Hanley and Rose (1987) studied the influence of forest overstories on snow depth and density in 33 stands over a 3-year period in the low-elevation, transient snow zone of southeastern Alaska. They attempted to use multiple regression analysis to develop predictive relations between snow depth and density (expressed as a proportion of depth and density in the open) and overstory variables that could be measured as part of a forest inventory. Eleven overstory variables were measured: tree density (number per unit area), percentage of spruce (by density), mean diameter at breast height (d.b.h.), coefficient of variation of d.b.h., mean tree height, coefficient of variation of tree height, gross wood volume, net wood volume, basal area, mean overstory canopy coverage (percentage), and even-aged or uneven-aged stands (a categorical variable). The effects of snow depth and density in the open also were included in the analysis. Of these variables, overstory canopy coverage and gross wood volume were the best predictors of relative snow depth (figs. 6 and 7). Forest overstory had very little effect on snow density.

From Hanley and Rose's (1987) study, it is apparent that snowpacks tend to be deeper under open-canopy stands than under closed-canopy stands and under low-volume stands than under moderate- or high-volume stands. The relations, however, were highly variable (figs. 6 and 7) and differed depending on snow conditions and storm characteristics. For example, at two different sampling times, the relative depths of two adjacent stands often were reversed (one time deeper in stand A than B, next time deeper in stand B than A) even though the overstories remained the same. The difference resulted from different weather conditions before, during, and after the snowstorm. High precision in predicting the effects of forests on snowpacks undoubtedly requires modeling of processes that control snow interception, accumulation, sublimation, and melt. The low precision of regressions based on stand attributes from forest inventory data makes it possible to generalize in only broad terms: open-canopy compared with closed-canopy stands. On a finer scale of resolution, the relations in figures 6 and 7 are of little value.

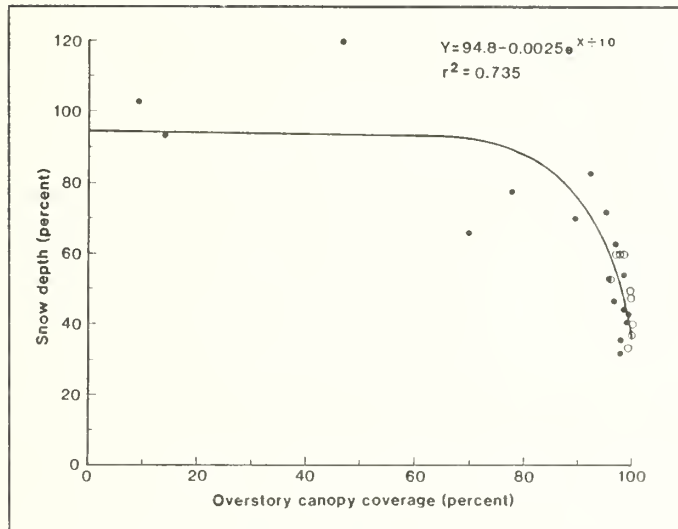


Figure 6—Snow depth in the forest (as a percentage of depth in the open) in relation to overstory canopy coverage. Canopy coverage was measured with a spherical densiometer. Open circles are even-aged stands; closed circles are old-growth stands. Each datum is the mean of five sampling periods (from Hanley and Rose 1987).

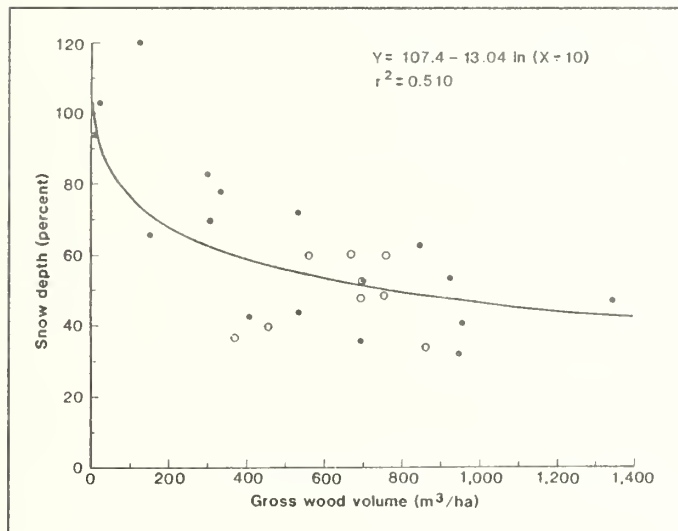


Figure 7—Snow depth in the forest (as a percentage of depth in the open) in relation to the gross wood volume of the forest overstory. Open circles are even-aged stands; closed circles are old-growth stands. Each datum is the mean of five sampling periods (from Hanley and Rose 1987).

Because most commercial-size stands have overstory canopy coverage greater than 95 percent (measured with a spherical densiometer, as in fig. 6) and gross wood volumes greater than 550 m³/ha (comparable to net volume of about 20,000 board feet per acre), it is not reasonable to base management decisions regarding projected snowpacks within commercial forest on the basis of stand inventory data. Hanley and Rose (1987) concluded that within the commercial hemlock-spruce forests, topographic setting (elevation, slope, aspect, shading from nearby mountains, susceptibility to cold-air drainage, distance from saltwater) probably is a more important determinant of snowpacks than is forest overstory. They suggested the following criteria for selecting stands for winter range for deer where snow accumulation is a problem: (1) topographic setting; (2) overstory canopy coverage at least 95 percent, as measured with a spherical densiometer; (3) net timber volume at least 20,000 board feet per acre; and (4) understory of relatively abundant, high-quality forage.

Forage Availability and Quality

Forage availability and quality are major factors determining the nutrition of deer. They affect diet composition and the intake of energy and nutrients. They are the critical link between forest management and population response of deer. Forage availability is primarily determined by the interaction of site and overstory on understory species composition and productivity (overstory-understory relations, discussed above), season of the year, burial by snow, and consumption and trampling by deer and other herbivores. Forage quality is primarily determined by plant species and part (for example, leaf or stem), stage of phenological development, and the environment in which the plant lives.

Seasonal changes in forage availability, digestibility, and chemical composition were studied by Hanley and McKendrick (1983, 1985) on Admiralty Island. The site was a low-elevation, old-growth, spruce-hemlock forest with a blueberry-dominated understory. Biomass of current annual growth peaked in late June through July (fig. 8). By the end of the winter and before spring growth, total biomass of current annual growth was about 20 percent of that in midsummer. Many herbaceous species are available only in the summer. Evergreen forbs (and the "half-shrubs" of fig. 6) persist through the winter but are frequently buried by snow. Shrubs, on the other hand, are available throughout the year, but they undergo major changes in the ratio of leaves to stems in current annual growth in the summer (fig. 9). The nutritional quality of leaves is much greater than that of stems (Hanley and McKendrick 1983).

The seasonal fluctuations in forage availability illustrated in figure 8 are more pronounced in forest openings and clearcuts, where summer production of total biomass, winter desiccation of evergreen herbs, and burial of vegetation by snow are greater than under forest overstories. Loss of forage through consumption by deer also increases the magnitude of seasonal fluctuations. It is most obvious in late winter and most evident by a reduction in the biomass of herbaceous species (especially bunchberry dogwood and trailing bramble) and the frequency of browsed blueberry stems. Over several years, however, deer can have a pronounced effect on the species composition and biomass of understory communities, especially those of even-aged stands where plants are trying to become established (Hanley 1987). For example, Hanley (1987) found a 25-fold difference in the total biomass of understory vegetation inside (782 kg/ha) and outside (31 kg/ha) a 21-year-old exclosure in an even-aged stand on southern Admiralty Island. This difference was much more pronounced than differences observed at any of the other three (old-growth) stands.

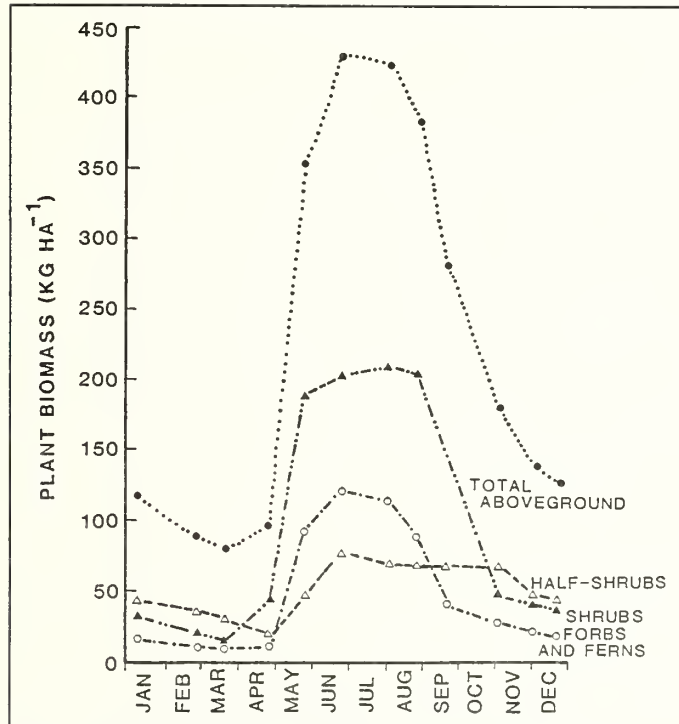


Figure 8—Monthly changes in plant biomass (current annual growth), January through December 1981, Admiralty Island. Half-shrubs are bunchberry dogwood, trailing bramble, and evergreen, decumbent blueberry species (from Hanley and McKendrick 1985).

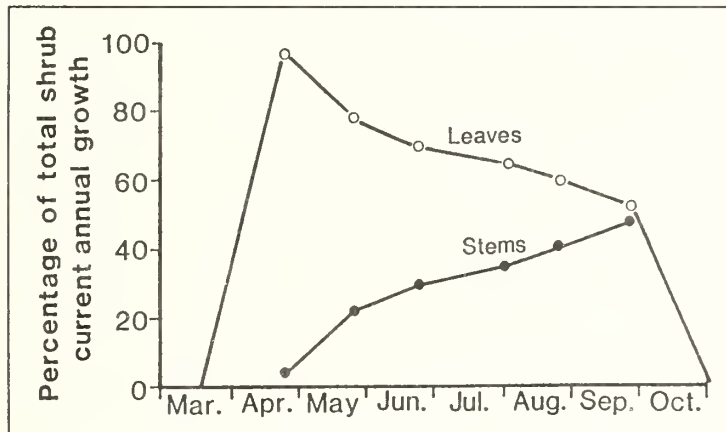


Figure 9—Monthly changes in the proportions of leaf and stem biomass (expressed as a percentage of total current annual growth) of Alaska blueberry during 1981 at the Admiralty Island study site (fig. 8) (from Hanley, unpublished data on file at Forestry Sciences Laboratory, Juneau, Alaska).

Forage quality also fluctuates greatly seasonally, generally paralleling the pulse of growth during the summer (fig. 10). Hanley and McKendrick (1983) studied seasonal changes in forage quality of 22 forages at the same study area on Admiralty Island where they studied seasonal changes in forage availability. They measured in-vitro dry-matter digestibility and the concentrations of neutral detergent fiber, acid detergent fiber, cellulose, lignin and cutin, total nitrogen, phosphorus, potassium, calcium, magnesium, sodium, copper, manganese, iron, and zinc. Their results were very similar to results from another study area on Admiralty Island and to other studies in southeastern Alaska and the Pacific Northwest. Forbs (including the "half-shrubs" of fig. 10) and, to a lesser degree, shrub leaves were consistently the most nutritious forages, especially in the winter. Seasonally low levels of digestible energy, nitrogen, and phosphorus were identified as the most important potential limitations of these forages in meeting the nutritional needs of deer and other herbivores.

One forage of potentially high energy value for deer is lichen, especially the beard lichens (*Alectoria sarmentosa* and *Usnea* spp.), which are common on slow-growing, open-grown trees or diseased and dead trees throughout the forest. In Hanley and McKendrick's (1983) analysis, in-vitro dry-matter digestibility of these lichens was very low, 15 to 26 percent, indicating a very low energy value for deer (digestible energy is roughly proportional to digestible dry matter). But lichens are known to be much more efficiently digested by rumen fluid from animals on a lichen-containing diet than from animals not on a lichen-containing diet. The source of rumen fluid used in these experiments was not exposed to lichens. In contrast, Robbins (1987) studied in-vivo digestibility of dry matter and protein of lichens (*A. sarmentosa*) fed to mule deer accustomed to eating lichens. Dry-matter digestibility was very high, 85.2 percent, but the very low crude protein concentration (2.0 percent) resulted in a negative apparent digestibility of protein (-218.0 percent). Metabolic fecal losses of nitrogen exceeded nitrogen intake. Thus, beard lichens are a very rich source of digestible energy for deer but are very unsatisfactory as a source of digestible protein.

Until recently, it has been extremely difficult to evaluate most of the natural forages consumed by deer in terms of their concentration of digestible protein. Concentration of crude protein can be determined easily (6.25 times the concentration of total nitrogen). But most of the natural forages consumed by deer contain tannins, which bind with protein and reduce its digestibility. The only way to estimate protein digestibility of such forages has been to conduct in-vivo digestion trials, requiring much time and great quantities of sample material.

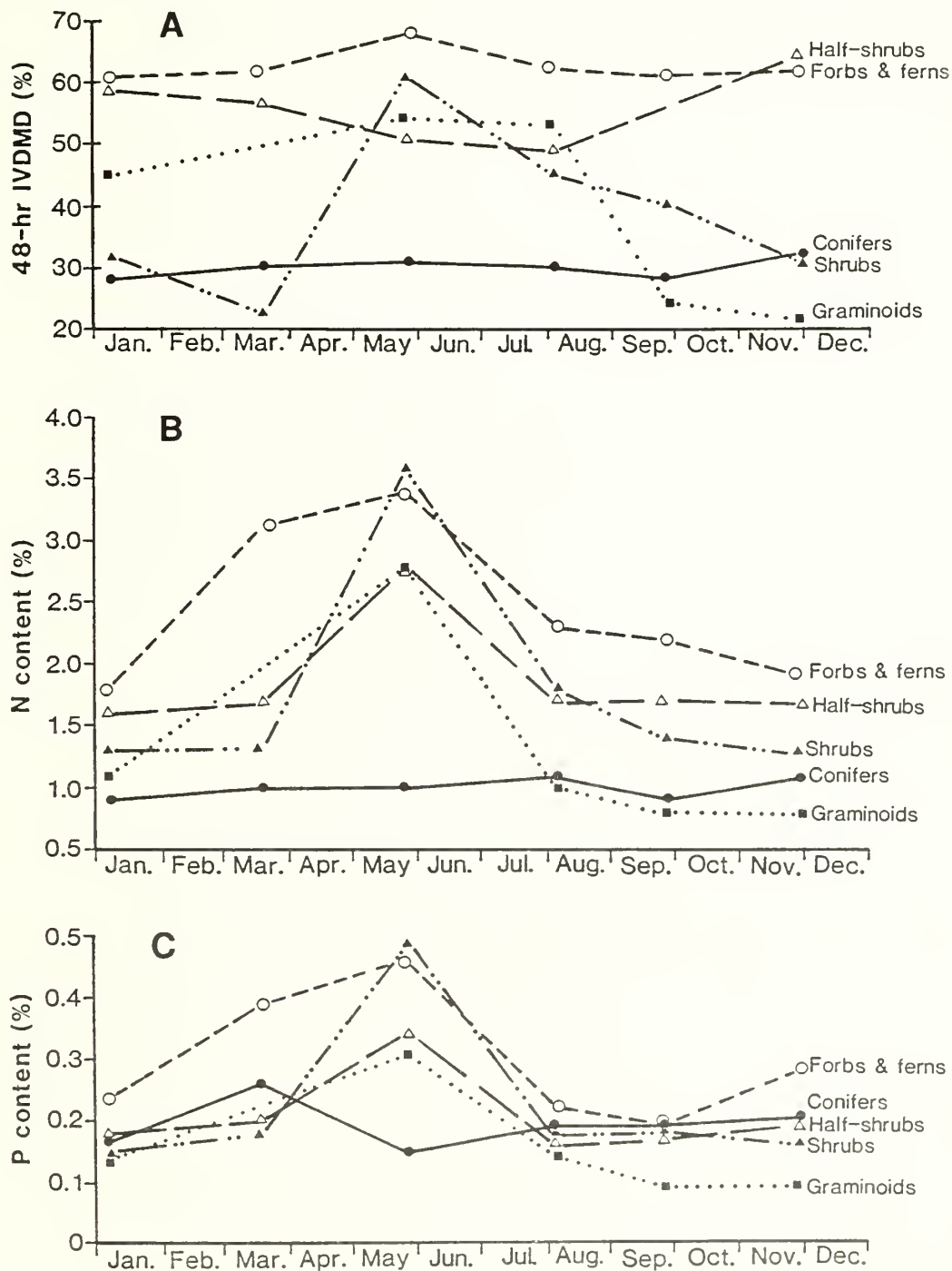


Figure 10—Seasonal changes in dry-matter digestibility and chemical composition of major understory species: A. In-vitro dry-matter digestibility (IVDMD). B. Nitrogen concentration. C. Phosphorus concentration. Half-shrubs are bunchberry dogwood, trailing bramble, and evergreen, decumbent blueberry species (from Hanley and McKendrick 1983).

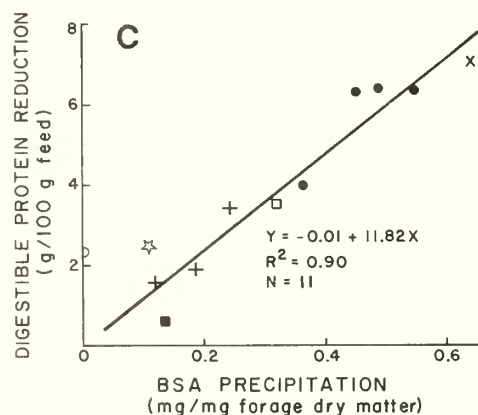
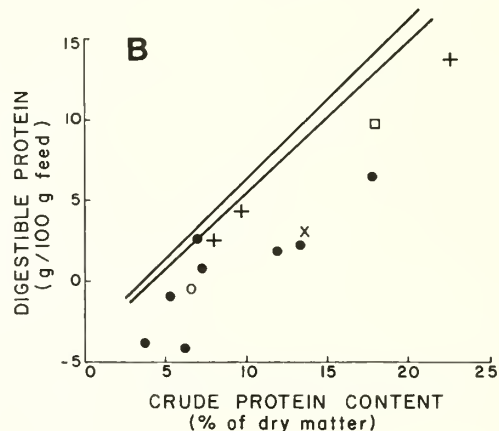
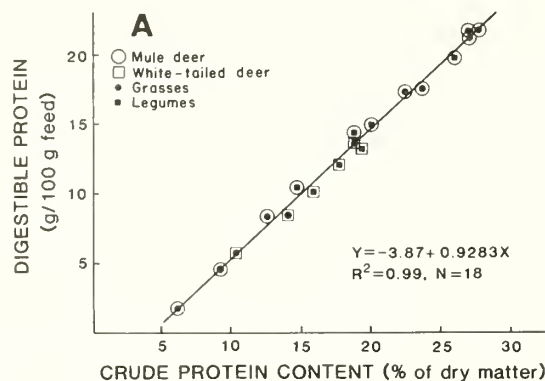


Figure 11—**A.** The relation between crude protein content and digestible protein content for feed for mule deer and white-tailed deer consuming grasses and agricultural legumes. **B.** Digestible protein in tree, shrub, and forb leaves, flowers, bark, or mixed feeds in which tannins may occur in significant amounts relative to the grass-legume regressions for elk (upper line) and deer (lower line). **C.** The in-vivo reduction in digestible protein because of tannins as a function of the bovine albumin serum (BSA) precipitating capacity of the forage (from Robbins and others 1987a).

'For grasses and agricultural legumes, which contain few tannins, digestible protein is a highly predictable function of crude protein (fig. 11A). The relation between protein digestibility and crude protein in deciduous browse stems collected in the winter is slightly lower, but not significantly different from that of grasses and legumes (Robbins and others 1987a). But in coniferous browse and leaves of trees, shrubs, and forbs, protein digestibility is significantly less than would be predicted for grasses and legumes (fig. 11B). Robbins and others (1987a), however, have recently shown that the reduction in protein digestibility because of tannins can be predicted by measuring the capacity of the forage to precipitate bovine serum albumin, a commercially available protein (fig. 11C). Digestible protein concentration of forages can now be estimated in the laboratory with small amounts of sample material.

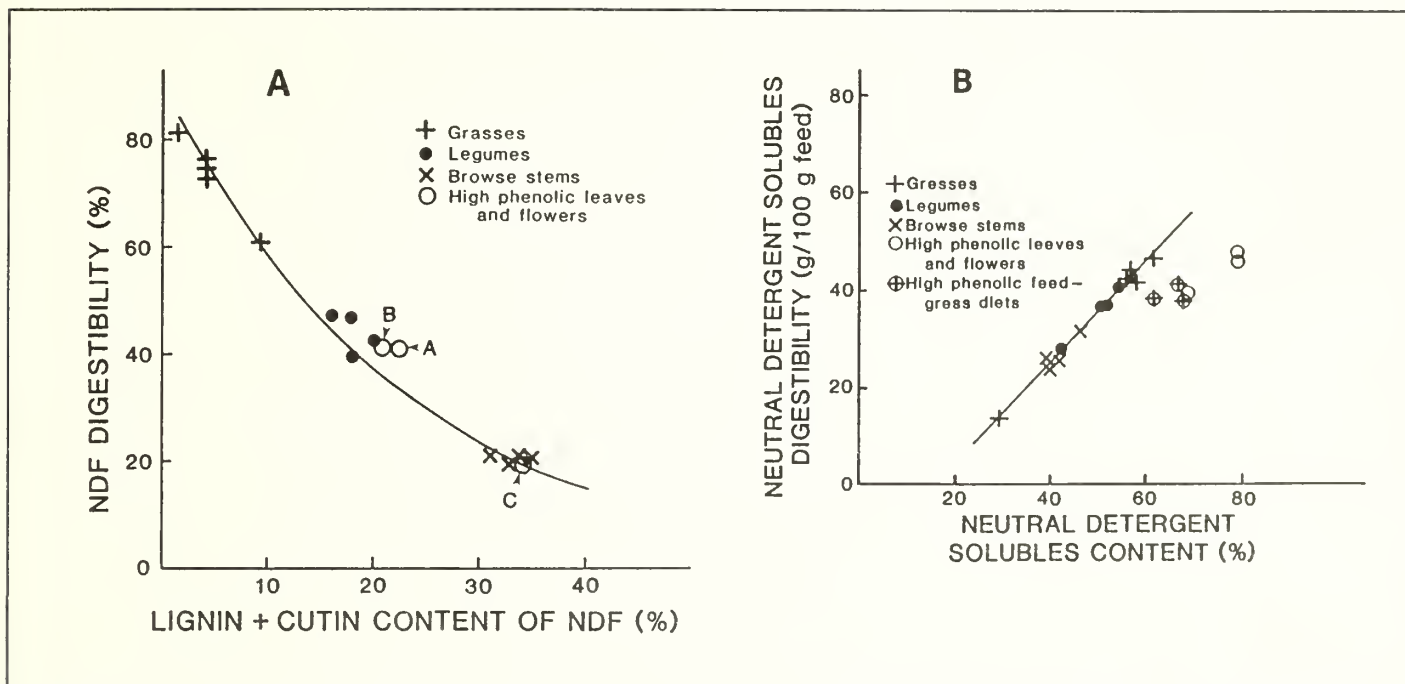


Figure 12—A. Digestibility of neutral detergent fiber (NDF) as a function of its content of lignin and cutin. B. Digestibility of neutral detergent solubles as a function of its content in the forage. The high-phenolic forages and diets are not included in the regression equations (from Robbins and others 1987b).

Because tannins reduce protein digestibility, they also reduce dry-matter digestibility and therefore affect the value of forage in terms of digestible energy as well as digestible protein. Until recently, however, whether tannins affect cell-wall digestibility or only the digestibility of the cell solubles has been unclear. Robbins and others (1987b) found that in mule deer, tannins do not affect cell-wall digestibility (fig. 12A) but do reduce the digestibility of cell solubles (fig. 12B) by about 2.8 units for every unit reduction in protein digestion. This contrasts with results from studies of domestic sheep and in-vitro digestion trials, where reduction in digestibility of cell wall has been shown. For deer, the summative equation developed by Robbins and others (1987b) should provide a more accurate estimate of in-vivo dry-matter digestibility than that provided by in-vitro digestion trials.

Compared with saliva of sheep and cattle, saliva of mule deer contains large amounts of proline-rich proteins that are highly effective at binding tannins and minimizing protein losses per unit of tannin. These tannin-salivary protein complexes should result in reduced digestibilities of both protein and neutral detergent solubles and, if completely effective, no reduction in cell-wall digestion. The proline-rich salivary proteins may also reduce the absorption of hydrolyzable tannins and the potential of tannin toxicity. Tannin toxicity may be an even greater factor affecting diet choices by ruminants than is reduction of digestibility (Robbins and others 1987a, 1987b).

Concentration of tannins (and other phenolics) can vary greatly within the same plant species, depending on the environment the plant is growing in. Hanley and others (1987) studied the chemical composition and nutritive value of blueberry and bunchberry dogwood leaves growing in a chronosequence of five stands on Chichagof Island during May through October. Three of the stands were young clearcuts (two were 5 years old, one of which had been burned after logging; one was 11 years old), and the two older stands were forests with well-developed overstories (one 80-year-old, even-aged stand and one 450-year-old, old-growth stand). Major differences in chemical composition of both species occurred between the young and older stands. Plants in the young stands had greater astringency (protein-precipitating capacity), concentrations of phenolics, and total nonstructural carbohydrates, but lower concentrations of nitrogen than did plants in the older stands. In-vitro dry-matter digestibility, however, did not differ among stands. Similar results were obtained for trailing bramble and skunkcabbage, which also were studied at the same time and place (Van Horne and others 1988). Chemical analyses of blueberry and bunchberry leaves collected in July from a clearcut and adjacent forest at another study area on Douglas Island indicated that concentrations of digestible protein were 2.0 to 2.3 times greater in leaves from the forest than those from the clearcut, though they did not differ in dry-matter digestibility (fig. 13).

These results are consistent with the hypothesis that plants growing in the shaded understories of forests in southeastern Alaska are essentially light-limited and allocate carbon (from photosynthesis) primarily to growth and maintenance. Plants growing in the open environments of young clearcuts, on the other hand, are probably light-saturated and accumulate sufficient carbon for growth and maintenance as well as relatively high concentrations of carbon-rich secondary compounds such as tannins and other phenolics (Hanley and others 1987).

In a palatability trial, deer distinguished between blueberry leaves from the forest and those from the clearcut and preferred (or at least ate more of) the leaves from the forest (Hanley and others 1987). But in a comparison of the chemical composition of blueberry and hemlock inside and outside four 19- to 21-year-old exclosures in forest understories, Hanley (1987) found no difference in in-vitro dry-matter digestibility or concentrations of nitrogen, phosphorus, neutral detergent fiber, and lignin as a proportion of acid detergent fiber. Therefore, although the palatability of plants to deer differs with their chemical composition (Hanley and others 1987) and deer may exert moderate to strong influence on the species composition and biomass of forest understories (Hanley 1987), their effect on dry-matter digestibility, fiber, nitrogen, and phosphorus concentrations of individual species may be negligible (Hanley 1987).

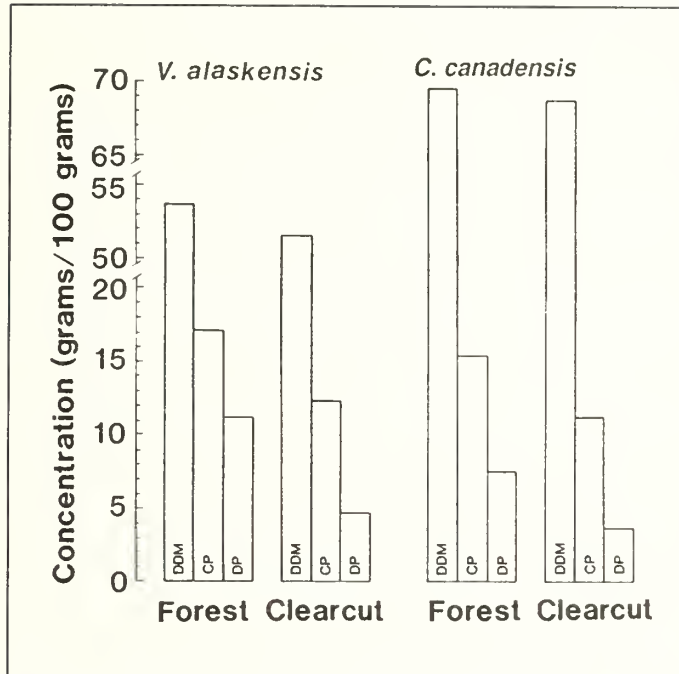


Figure 13—Concentrations of digestible dry matter (DDM), crude protein (CP), and digestible protein (DP) on a dry-matter basis in leaves of Alaska blueberry (*Vaccinium alaskensis*) and bunchberry dogwood (*Cornus canadensis*) from an old-growth forest and an adjacent 8-year-old clearcut in July near Juneau, Alaska (from Hanley and others, in press). Based on data from Hanley and others (1987a); DDM calculated with equation from Robbins and others (1987b); DP calculated with equation from Robbins and others (1987a).

Diet Composition and Energy Intake

The composition and quality of diets selected by deer vary with changes in forage availability and quality and the nutritional status of the animal. Dietary composition and total intake of dry matter determine nutrient and energy intake.

It is impossible to accurately measure either diet composition or dry-matter intake of wild deer in southeastern Alaska. Deer are seldom visible at close enough range to see what they are eating and how fast they are eating it. Analyses of rumen and fecal samples yield results biased toward overestimating the least digestible and most recognizable plant species and parts (Hanley and others 1985). For example, conifers tend to be overrepresented and forbs underrepresented in fecal samples relative to rumen samples (fig. 14), and the same can be said about rumen samples relative to actual diets. Qualitatively, however, rumen and fecal samples can provide insight into relative changes in diet composition and quality over time.

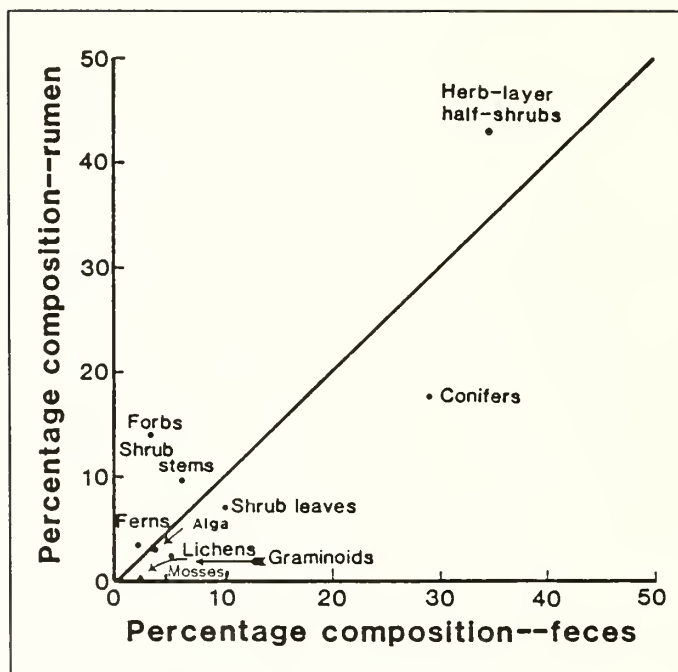


Figure 14—Composition of deer rumen contents relative to composition of deer feces on a dry-weight basis. Data are means from 13 deer shot during January through March on Admiralty Island and Chichagof Island during mostly snow-free conditions. Herb-layer half-shrubs are bunchberry dogwood, trailing bramble, and evergreen, decumbent blueberry species. The line indicates a 1:1 relation (data from Hanley and others 1985).

Hanley and McKendrick (1985) studied diet composition of deer in the same low-elevation, old-growth stands on Admiralty Island where they studied seasonal changes in forage availability and quality. By weighting the species composition of deer feces (table 2) by the estimated dry-matter digestibility of the respective plants, they obtained an estimate of the monthly changes in diet composition of deer in their study area (fig. 15). Throughout the year, herbs (primarily forbs) were eaten in greatest abundance, except when buried with snow. Shrub leaves (primarily blueberry and devilscub) were eaten mostly in the spring when the leaves were young and growing rapidly and again in the fall when herbaceous biomass declined at the end of the growing season (fig. 8). Blueberry stems and western hemlock were most important when snow buried the herbs. This apparent preference of deer for herbs over shrubs over conifers throughout the year is the pattern that would be expected on the basis of the relative nutritional qualities of these respective forage classes (fig. 10).

Table 2—Mean composition (dry weight) of deer feces at the Admiralty Island study site^a

Forage class and species	1980, ^b Dec.	1981 ^c			
		Jan.-Mar.	Apr.-June	July-Sept.	Oct.-Dec.
		Percent			
Forbs and ferns:					
<i>Athyrium filix-femina</i>	0	tr(0)	2(1)	0	0
<i>Blechnum spicant</i>	0	1(1)	tr(0)	0	4(4)
<i>Coptis asplenifolia</i>	0	tr(0)	tr(0)	1(1)	1(0)
<i>Cornus canadensis</i>	2	33(2)	26(8)	14(2)	19(7)
<i>Listera</i> spp.	0	0	0	1(1)	tr(0)
<i>Lysichiton americanum</i>	0	5(1)	2(1)	16(5)	4(2)
<i>Maianthemum dilatatum</i>	0	0	0	1(1)	0
<i>Osmorhiza</i> spp.	0	0	2(1)	4(3)	1(0)
<i>Rubus pedatus</i>	1	23(1)	11(3)	20(3)	21(7)
<i>Streptopus</i> spp.	0	0	tr(0)	tr(0)	1(1)
<i>Tiarella trifoliata</i>	0	3(1)	tr(0)	5(2)	9(3)
Others ^d	0	2(1)	tr(0)	1(0)	9(2)
Unknown	0	1(1)	4(2)	1(1)	2(0)
Shrubs:					
<i>Alnus</i> spp.	tr	1(1)	1(1)	10(3)	4(3)
<i>Ledum palustre</i>	0	0	0	tr(0)	0
<i>Menziesia ferruginea</i>	0	0	1(1)	3(0)	1(1)
<i>Oplopanax horridum</i>	0	0	13(8)	8(0)	1(1)
<i>Vaccinium</i> spp. ^e	39	6(2)	18(9)	1(0)	3(1)
Unknown	0	1(1)	1(1)	0	2(2)
Conifers:					
<i>Picea sitchensis</i>	2	tr(0)	tr(0)	tr(0)	tr(0)
<i>Pinus contorta</i>	0	tr(0)	0	0	tr(0)
<i>Tsuga heterophylla</i>	48	16(1)	9(4)	4(1)	10(7)
Graminoids:					
<i>Deschampsia caespitosa</i>	0	0	tr(0)	0	1(1)
<i>Carex</i> spp.	0	0	1(1)	1(0)	tr(0)
<i>Elymus arenarius</i>	1	tr(0)	1(1)	1(0)	tr(0)
Other	0	0	tr(0)	1(0)	1(0)
Lichens:					
<i>Alectoria</i> spp. or <i>Usnea</i> spp.	tr	tr(0)	tr(0)	1(1)	2(1)
<i>Lobaria</i> spp.	6	3(0)	2(1)	1(1)	3(0)
Other	0	tr(0)	0	0	0
Alga:					
<i>Fucus furcatus</i>	tr	2(0)	2(1)	1(0)	1(0)
Mosses:					
<i>Hylocomium splendens</i> or <i>Rhytidiadelphus loreus</i>	1	4(0)	3(1)	2(1)	2(0)
<i>Sphagnum</i> spp.	0	1(1)	tr(0)	1(0)	2(1)
Others	0	1(1)	tr(0)	1(0)	2(1)

^a Adapted from Hanley and McKendrick (1985).

^b Only December 1980 reflects the presence of snow.

^c tr = trace = <0.5 percent; number in parentheses is standard error of monthly samples combined in calculating means.

^d *Dryopteris dilatata*, *Gymnocarpium dryopteris*, *Monesis uniflora*, *Polypodium vulgare*, *Pyrola secunda*, and *Viola glabella*.

^e Includes *V. alaskensis*, *V. ovalifolium*, and *V. parvifolium*.

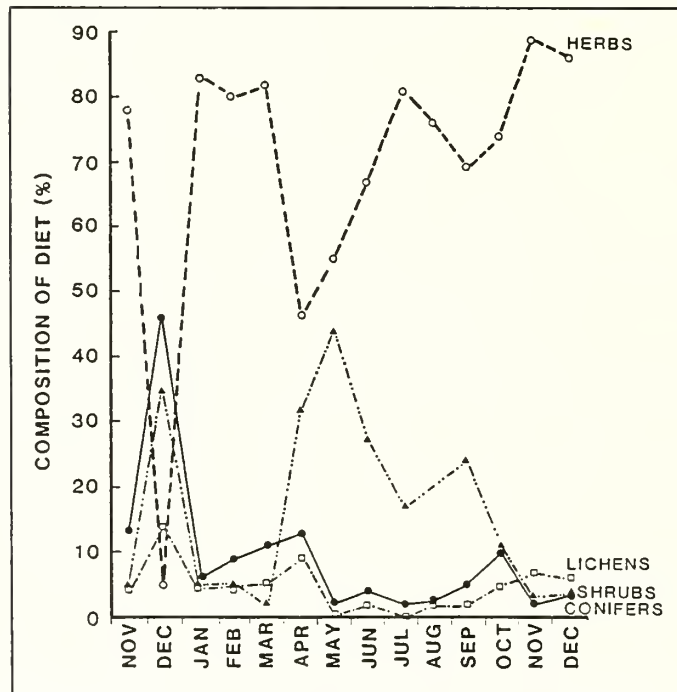


Figure 15—Estimated monthly diet composition of deer at the Admiralty Island study site, November 1980 through December 1981. Values are based on fecal composition data adjusted for in-vitro dry-matter digestibility. Only values for December 1980 reflect the presence of snow (from Hanley and McKendrick 1985).

By combining the estimates of diet composition (fig. 15) with the data for dry-matter digestibility and chemical composition (fig. 10), Hanley and McKendrick (1985) obtained monthly estimates of dry-matter digestibility and chemical composition of deer diets in their study area (fig. 16). Results indicated the great value of herbs in the winter energy budget of deer: When they were buried with 20 cm of snow, the estimated dry-matter digestibility of the diet dropped from about 58 to 38 percent. Dry-matter digestibility of the summer diet, however, was relatively low compared with diets probably obtained in subalpine habitats where deer cabbage (with in-vitro dry-matter digestibility of 78.6, Hanley and McKendrick 1983) is a major dietary component. On the basis of crude protein concentrations (fig. 16B) and the results of the studies by Robbins and others (1987a) and Hanley and others (1987), concentrations of digestible protein probably were adequate year-around for both maintenance and lactation requirements. Phosphorus concentrations, on the other hand, varied from superabundance in spring and early summer to submarginal levels in late summer and fall. That deer probably are able to store phosphorus in spring and mobilize it from reserves in fall seems reasonable, however.

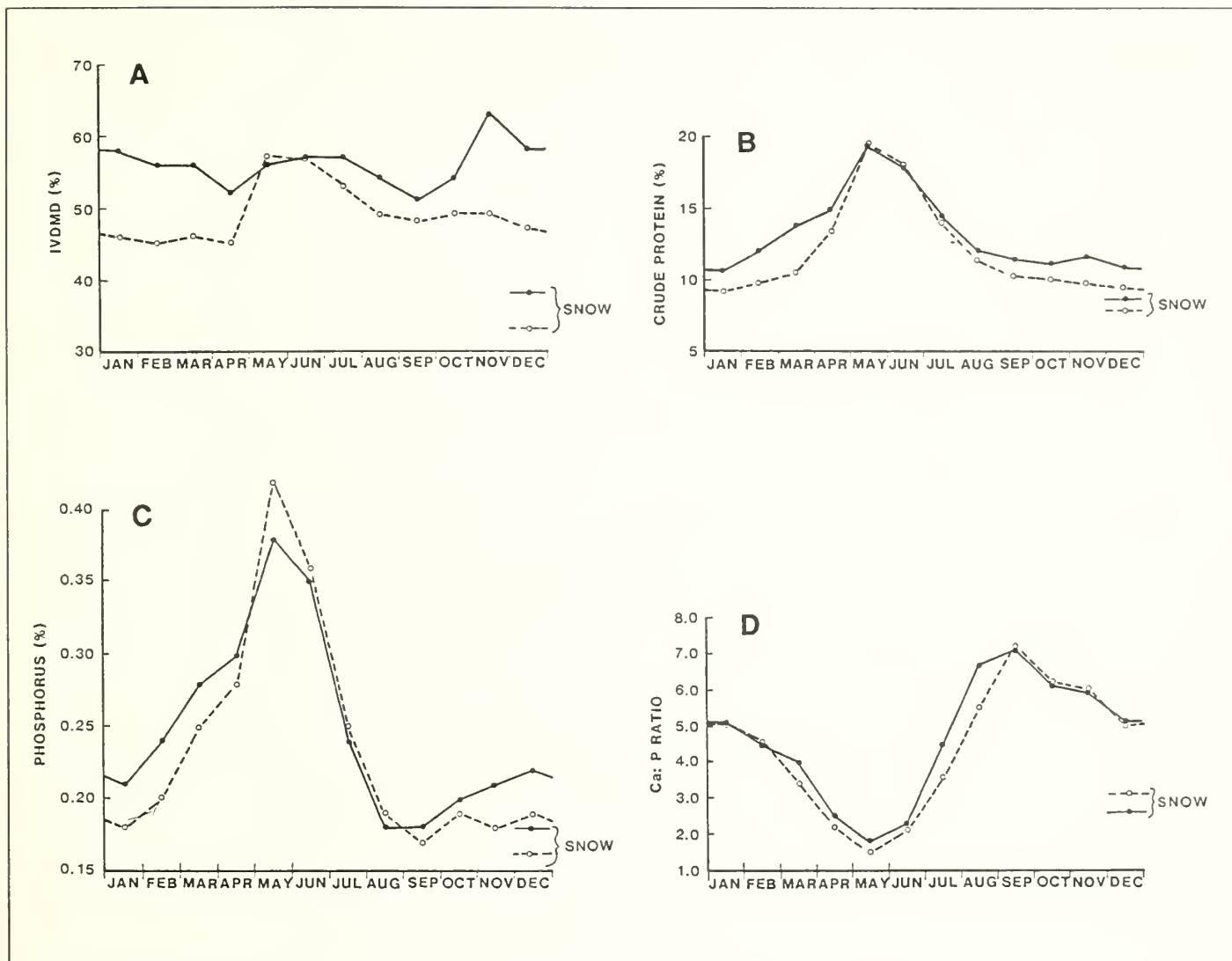


Figure 16—Monthly estimates of dry-matter digestibility and chemical composition of deer diets (solid circles and line) and mean of total available forage in the habitat (open circles and broken line) at the Admiralty Island study site, 1981. All values are for snow-free conditions except where indicated for the month of December (from Hanley and McKendrick 1985). **A.** In-vitro dry-matter digestibility (IVDMD). **B.** Crude protein. **C.** Phosphorus. **D.** Calcium:phosphorus ratio.

Although the analysis above and that by Hanley and others (1987) indicate that digestible protein probably is not a limiting factor for deer in forest habitats, the situation may be quite different in clearcuts. There, the combination of lower concentrations of crude protein and higher concentrations of tannins may result in a diet that meets only about half the digestible protein requirement of a lactating doe (Hanley and others 1987). The problem, however, is more complicated than simply the digestible protein concentration of the forage. It also depends on the total daily intake, which is affected by ingestion rates and rumen turnover rates and whether the deer is time- or bulk-limited in its daily intake of dry matter.

The rate at which a deer can ingest food while foraging is important because it determines the animal's time constraints and, therefore, its ability to be selective in what it eats. Usually, the best foods are relatively uncommon in most habitats. Even where the same desirable species occurs in a large patch and high biomass (for example, deer cabbage in subalpine habitats), not all potential bites are of equal value. Some leaves are more succulent and nutritious than others. The deer's ability to find the best bites determines the quality of its diet. But the rate at which it takes in food and the time available for foraging determine its total daily intake. Time spent searching for the best bites is time lost for eating, except when chewing and searching occur together. Time spent ruminating and waiting for digesta to pass from a full rumen also is time lost for feeding. The optimization problem faced by a foraging deer, therefore, is one of balancing the tradeoffs between search time, ingestion rates, rumen turnover rates, and dietary quality if it is to obtain the maximum daily intake of digestible energy and nutrients.

Wickstrom and others (1984) studied ingestion rates of mule deer and elk. (Elk provide an insightful comparison because they are so much larger than mule deer: 143-194 kg compared with 32-52 kg for Wickstrom's animals; see Hanley (1982) for implications.) They were particularly interested in determining the relations between dry-matter intake rates and food biomass and bite size. They found that the relation between food biomass and intake rate was asymptotic, with the asymptote (maximum rate of intake) occurring at surprisingly low levels of biomass (<50 kg/ha) for deer (fig. 17). The asymptote occurred at much higher levels for elk. For both species, however, asymptotic intake rates were clearly a function of bite size (fig. 18). Spalinger and others (1988) conducted similar experiments with Sitka black-tailed deer under more tightly controlled conditions in pens and found similar results, except that asymptotic intake rates were reached at about 5 kg/ha of food biomass. This means that for deer, food biomass is a relatively unimportant factor affecting intake rates and, presumably, diet composition at all but extremely low levels of biomass. Bite size (mostly dependent on leaf or stem size and homogeneity) is much more important than biomass. Other factors, however, also may be important; for example, clumping of plants may effectively increase the food biomass experienced by a deer as it moves from patch to patch. Increased biomass of undesirable species, on the other hand, probably decreases searching efficiency (Spalinger and others 1988). Food biomass, per se, is a much more important factor for elk than for deer.

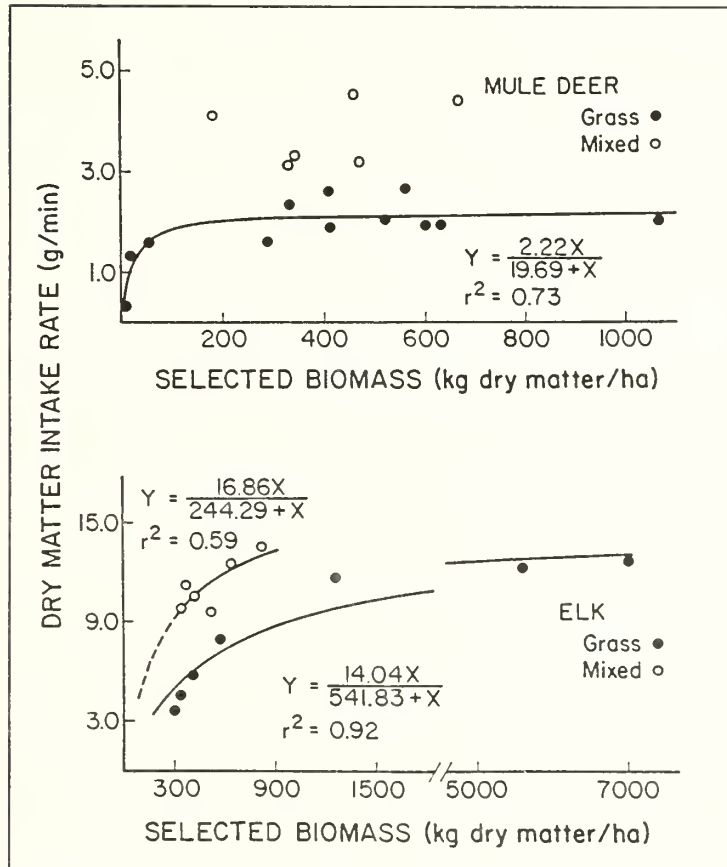


Figure 17—Dry-matter intake rate as a function of forage biomass for mule deer and elk consuming grasses and mixed diets. Mule deer intake was asymptotic in the mixed communities over the entire range of biomass (from Wickstrom and others 1984).

Asymptotic intake rate is a function of bite size (or leaf size) because a deer cannot bite and chew at the same time. A greater proportion of time is spent biting and a smaller proportion spent chewing when a deer is feeding on small-leaved plants than on large-leaved plants. Asymptotic intake rates, therefore, are lower for small-leaved than for large-leaved plants (Spalinger and others 1988).

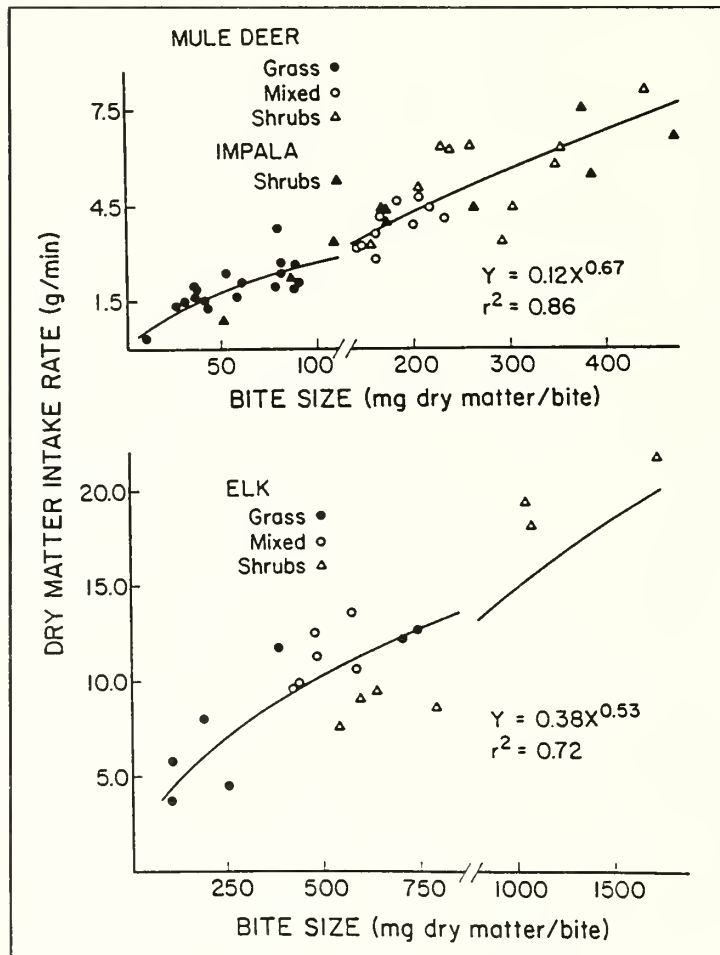


Figure 18—Dry-matter intake rate as a function of bite size for mule deer, elk, and impala consuming grasses, shrubs, and mixed diets (from Wickstrom and others 1984).

There also is a trade-off between bite size and biting rate: As bite size increases, biting rate decreases (fig. 19) because more time is needed for chewing. As food biomass decreases, the animal must travel at a faster rate between bites (fig. 20). With large bites, the time spent traveling between bites can be spent chewing, so no time is lost for feeding (Spalinger and others 1988). Under low biomass situations, therefore, fewer but larger bites are preferable to more but smaller bites. Leaf size is a very important factor affecting intake rates and, consequently, diet quality, especially at low levels of food biomass.

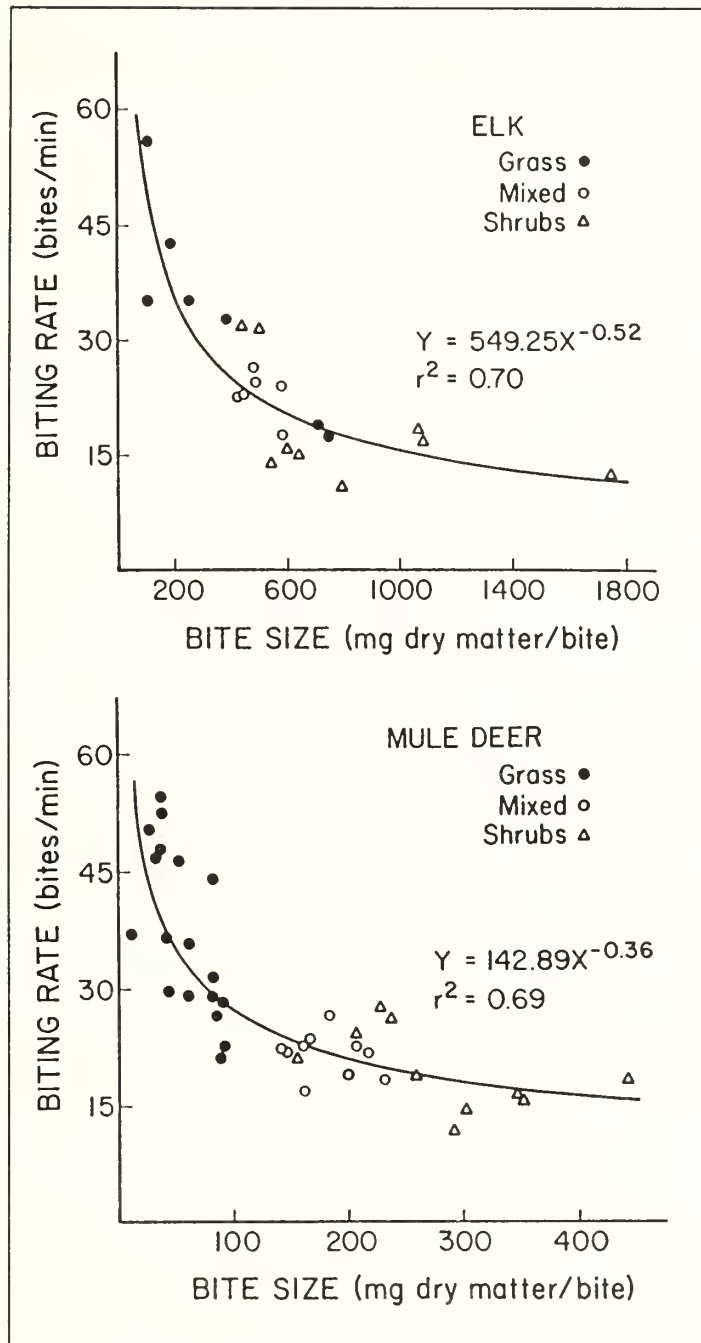


Figure 19—Biting rate as a function of bite size for mule deer and elk consuming grasses, shrubs, and mixed diets (from Wickstrom and others 1984).

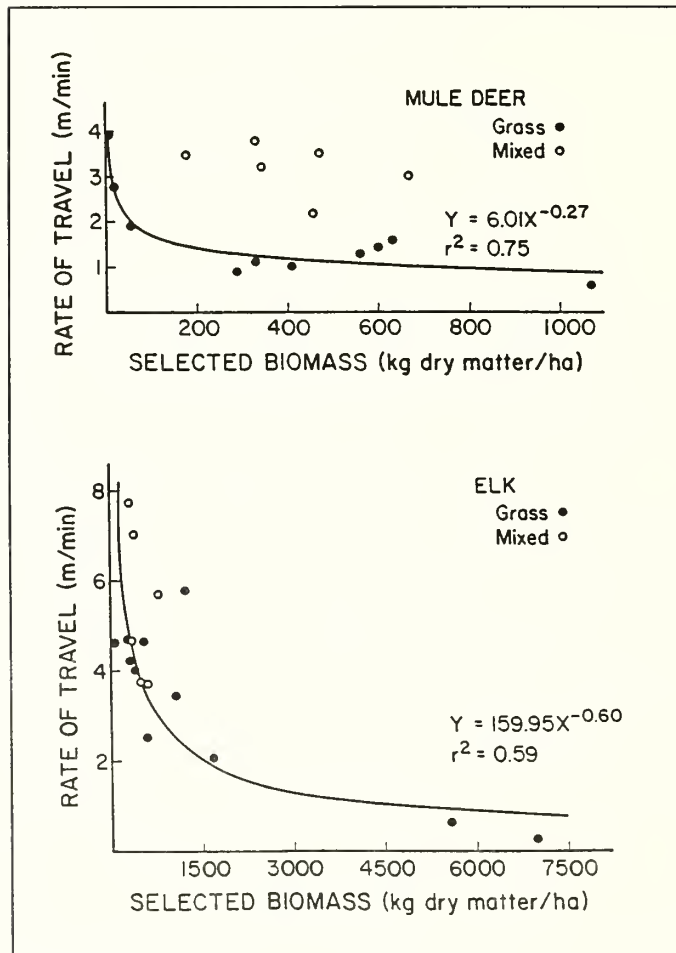


Figure 20—Travel rate of mule deer and elk foraging in grass and mixed communities as a function of forage biomass (from Wickstrom and others 1984).

Forages also differ in their rate of breakdown and passage from the rumen (fig. 21). Rumen turnover rates are important, especially to deer (Hanley 1982), because slow-passing food can result in bulk-limitations to daily dry-matter intake. Spalinger and others (1986) studied the physical and chemical characteristics of plants and determined the breakdown rate and passage from the rumen of mule deer and elk. The most important forage characteristic was the mean thickness of the plant cell walls (which covaried, positively, with neutral detergent fiber). As cell-wall thickness increased, mean retention time increased (or breakdown and rumen turnover rates decreased) (fig. 22). The relation was not linear, however, but instead tended toward asymptotic. This means that rumen retention time should increase rapidly, but at a decreasing rate, as cell-wall thickness increases.

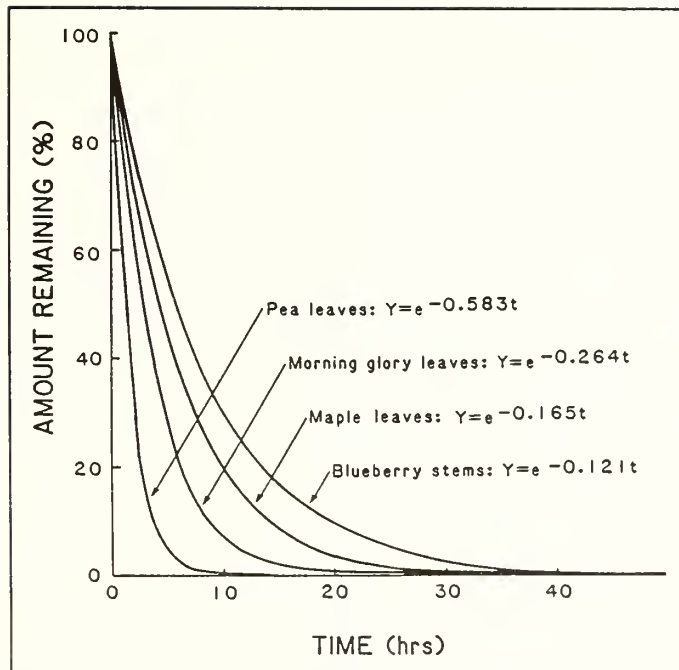


Figure 21—The relative breakdown rates of large (2.8 to 4.0-mm) particles of four forages in the rumen of mule deer and elk (from Spalinger and others 1986).

Deer, therefore, given the opportunity to select from a wide range of plants of high nutritional quality (usually of low cell-wall thickness), should base their selections more on cell-wall thickness than simply on dry-matter digestibility or chemical composition. When available forage is of greater cell-wall thickness, such as would occur in the winter, the selection of forage should be based more on digestibility than on cell-wall thickness because rumen retention time becomes nearly asymptotic at higher cell-wall thicknesses. Retention times are considerably greater in the latter case, however, and should result in a reduction in both foraging time and forage intake (Spalinger and others 1986). Throughout the year, when thin cell-walled plants (low concentrations of neutral detergent fiber) are available, they should be preferred forages unless they are too-small-bite size or contain high levels of toxic compounds.

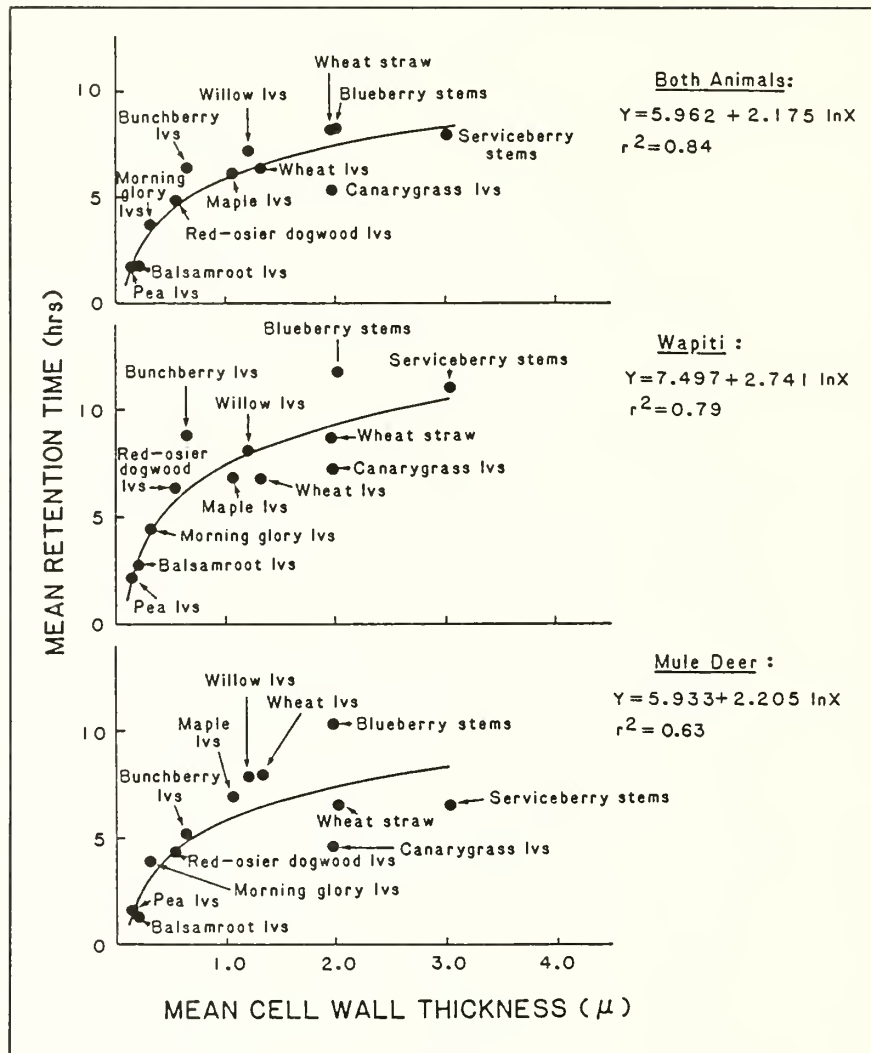


Figure 22—The relation between mean retention time of large particles in the rumen of mule deer and elk and their mean cell-wall thickness (excluding the cuticle); "lvs" is leaves (from Spalinger and others 1986).

Energy Expenditure

Deer experience different energy costs of foraging in different habitats depending on slope steepness, snow depth, obstacles (for example, fallen trees or logging slash), thermal characteristics of the habitat, and the deer's rate of travel. Of these, snow depth is usually most significant.

Parker and others (1984) studied energy expenditures for locomotion by mule deer and elk. Energy cost of locomotion through snow increased exponentially with increasing sinking depth and also increased with snow density (fig. 23). When sinking depth was expressed as a percentage of brisket height, equations for both deer and elk were identical. When sinking depths reached carpus height, costs of locomotion increased dramatically. Brisket and carpus heights, of course, are very different for deer than for elk and vary with animal body weight (fig. 24). For sinking depths

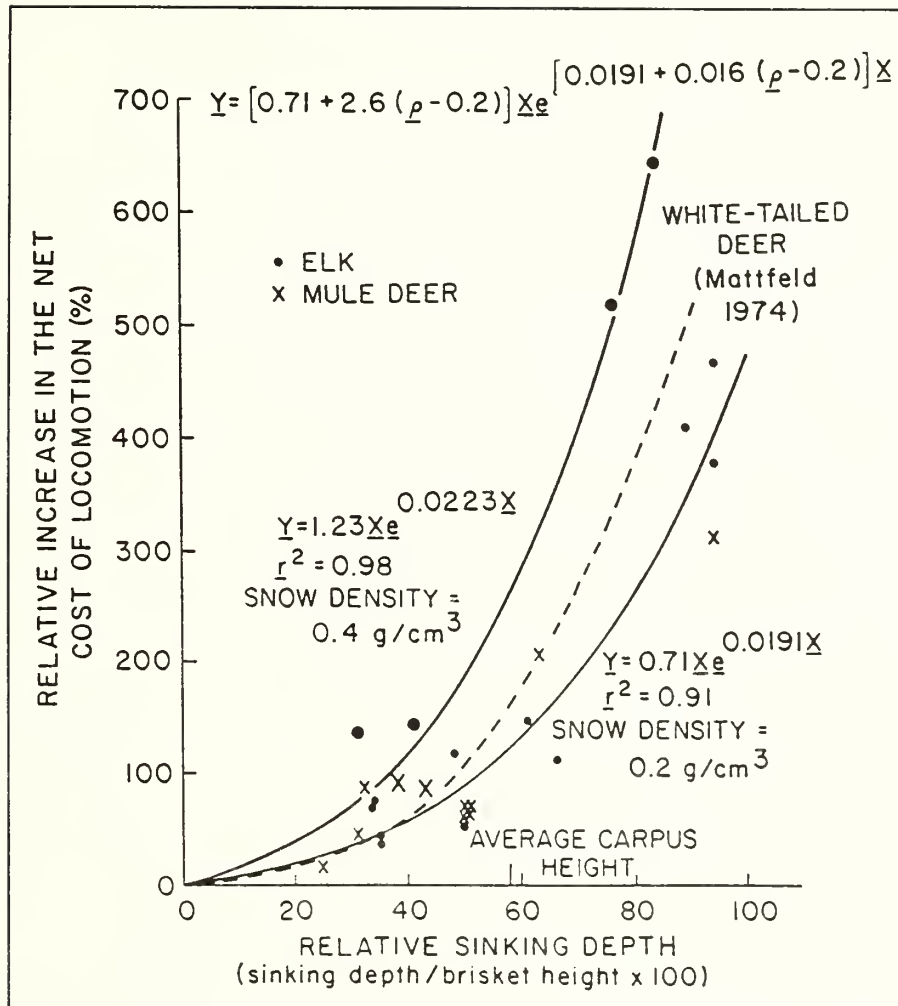


Figure 23—The relative increase in the net cost of locomotion in snow of two densities (large symbols = 0.4 g/cm^3 , small symbols = 0.2 g/cm^3) as a percentage above the cost of travel without snow as a function of relative sinking depth for mule deer and elk. Dashed line represents a similar function for white-tailed deer. The larger equation predicts the relative increase in energy expenditure (Y) for locomotion in snow of a given density (p) and relative sinking depth (X) (from Parker and others 1984).

greater than brisket height, mule deer and elk resorted to exaggerated bounding gaits that greatly increased energy expenditures because of vertical displacement of the entire body mass (Parker and others 1984). For a black-tailed deer with a body weight of 50 kg, therefore, two important thresholds in snow depth would occur at about 30 cm (carpus height) and 55 cm (brisket height).

Although it was not possible to measure energy expenditure for locomotion through logging slash, Parker and others (1984) evaluated the potential effects of logging slash by modeling the process. They made the following assumptions: (1) slash deposition is uniform so that impediments, including logs and branches, are equal in size;

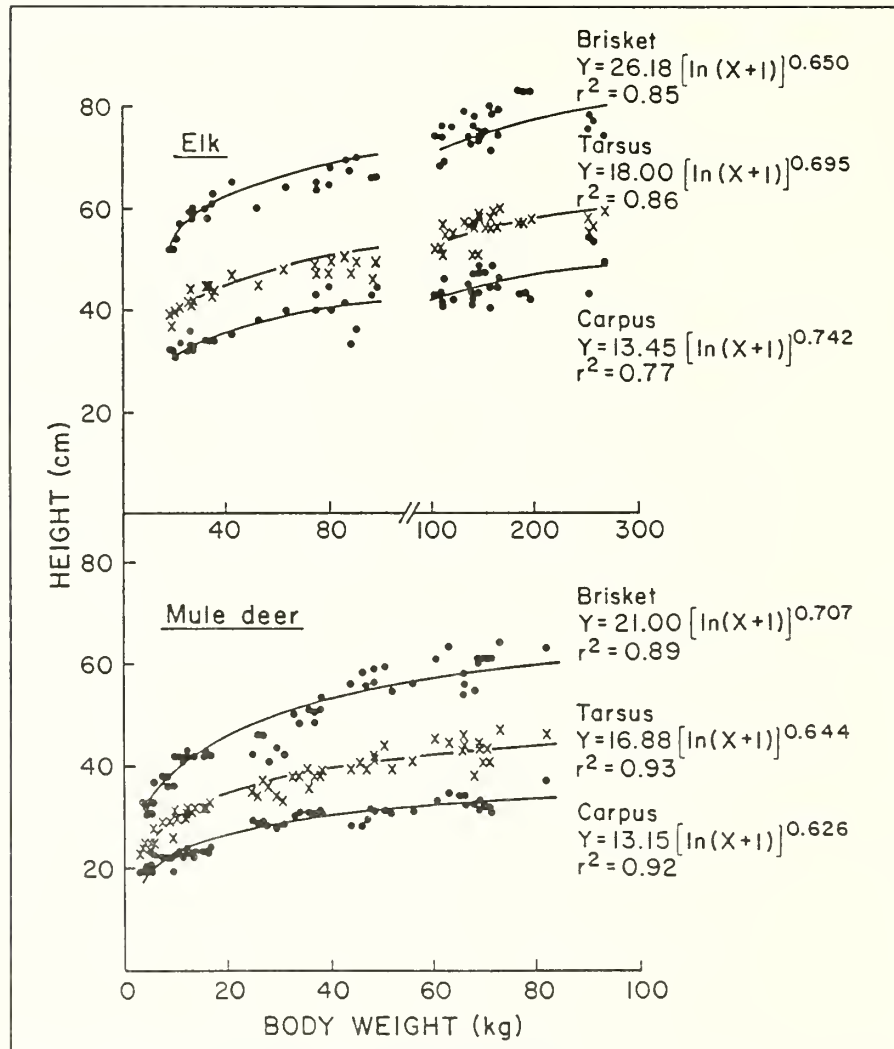


Figure 24—Brisket, tarsus, and carpus heights as a function of body weight for mule deer and elk (from Parker and others 1984).

(2) between obstacles, the energy cost to the animal is equal to that of horizontal locomotion; (3) for debris less than 50 percent of brisket height in diameter, the animal simply lifts its legs higher during travel and energy expenditure is similar to that of locomotion in dense snow; (4) for debris greater than 50 percent of brisket height in diameter, the animal jumps over obstacles and energy expenditure is estimated at 5.9 kcal per kg per vertical meter; and (5) during jumping, animals are assumed to fold their legs up to 50 percent of brisket height and to clear all obstacles by 0.15 m.

The modeling results (fig. 25) indicated that at slash depths less than that required for jumping to clear obstacles, additional energy costs for travel through slash were virtually insignificant at up to 50 obstacles per 100 m traveled. When slash depths were great enough to require jumping, however, energy costs of locomotion increased dramatically and in direct proportion to the number of obstacles and their

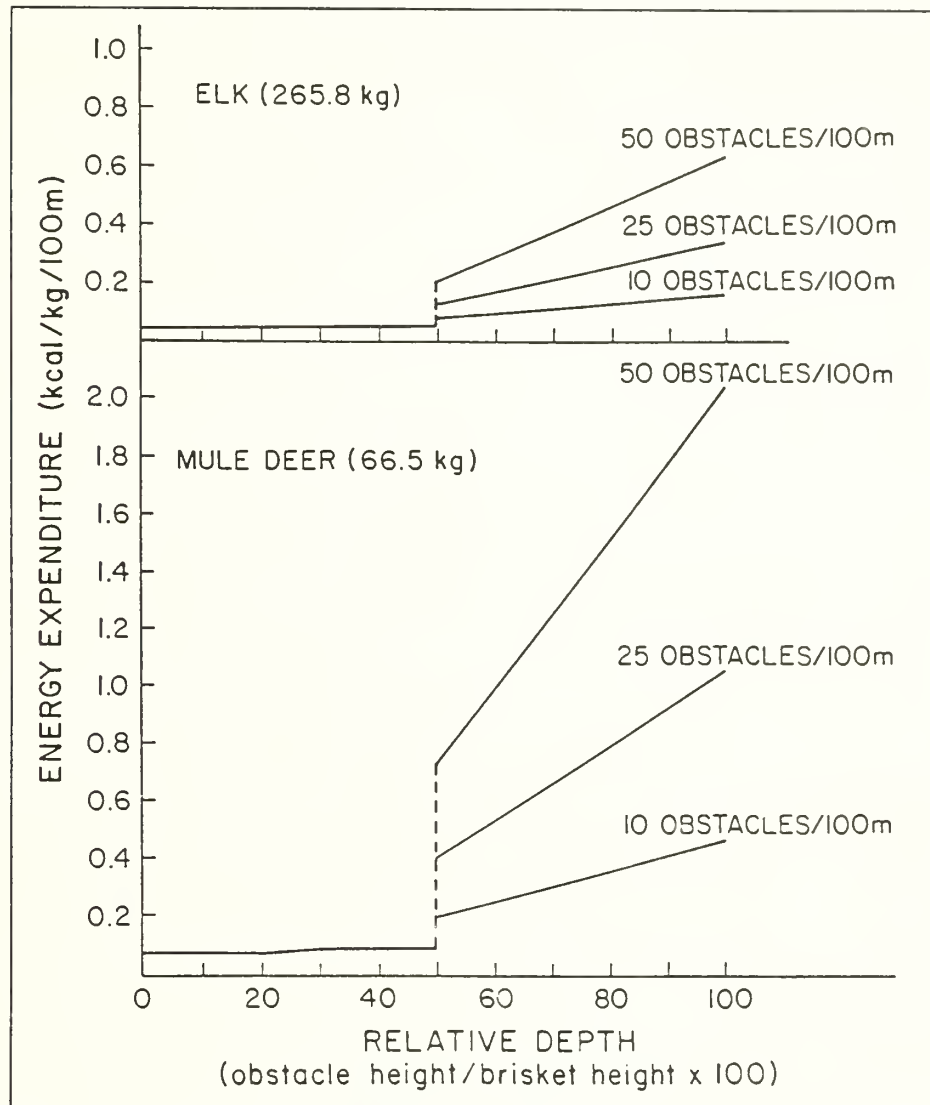


Figure 25—Predicted energy expenditures of locomotion (that is, the posture of locomotion plus the net cost) through slash deposits of varying densities as a function of relative depth for a 265.8-kg elk and a 66.5-kg mule deer (from Parker and others 1984).

heights. These estimates, of course, would be too low when shrubs and young conifers also interfere with movement and would be too high when deer meander around obstacles rather than jumping over them. They are most useful for providing estimates of potential relative differences in energy costs for deer resulting from various alternatives for slash management. The actual costs for deer will depend on additional factors, most important of which are shrub density and deer behavior. Slash is never of uniform depth and density.

Energy costs of locomotion (kilocalories per kilogram per kilometer) vary with the animal's body weight, whether for horizontal, upslope, or downslope locomotion, and also vary with the speed of travel (Parker and others 1984). Although these costs become important from the standpoint of foraging efficiency, alone they have few implications for management.

The other major environmental factor affecting energy expenditure is the thermal environment. Parker and Robbins (1984) studied energy costs for thermoregulation in mule deer and elk. Although most studies of thermoregulation by animals have been done indoors in metabolic chambers, Parker and Robbins did their study outdoors under more realistic conditions actually experienced by wild animals. By calculating an "operative" temperature (incorporating the thermal consequences of air temperature, windspeed, and thermal radiation), they were able to relate their measures of energy expenditure to a single variable. In a metabolic chamber, the operative temperature would be equal to the air temperature.

Parker and Robbins (1984) were able to determine limits of the thermoneutral zone for deer and elk in both winter (fig. 26) and summer (fig. 27). The thermoneutral zone is the range of operative temperatures within which the animal does not have to expend additional energy to maintain a constant body temperature. As temperatures increase above, or decrease below, the thermoneutral zone, the animal must spend additional energy for thermoregulation. Thermally critical environments (outside the range of the thermoneutral zone) for mule deer occurred at operative temperatures of less than -20°C and greater than 5°C in winter and greater than 25°C in summer. Perhaps the relatively low upper critical limit for deer in winter (5°C) is a principal reason why deer seem to prefer to winter as high as possible, just below the snow-line, in southeastern Alaska. Energy expenditures increased for elk at operative temperatures below -20°C and above $+20^{\circ}\text{C}$ in winter; metabolic rates decreased between 10 and -20°C . A major difference between elk and mule deer in the summer is that elk rely heavily on cutaneous evaporation of water (sweat) for cooling, whereas deer rely on panting as their primary means of heat dissipation. In the humid coastal environments of southeastern Alaska, however, evaporative heat loss may be less efficient by either means (and, therefore, the upper critical temperatures may be lower) than in eastern Washington where Parker and Robbins did their work.

Some weather conditions, therefore, are clearly outside or clearly within the thermoneutral zones of deer and elk. But the thermal environment experienced by an animal varies greatly from place to place. For example, whether the animal is in the sun or shade, standing or lying, exposed to or sheltered from the wind, all have large influences on the operative temperature experienced by the animal. From a management perspective, the thermoneutral zone provides only a rough idea of when an environment may or may not be thermally stressful to an animal. It provides some insight into the environmental factors influencing animal behavior, but the high variability of microclimate within habitats complicates its practical usefulness.

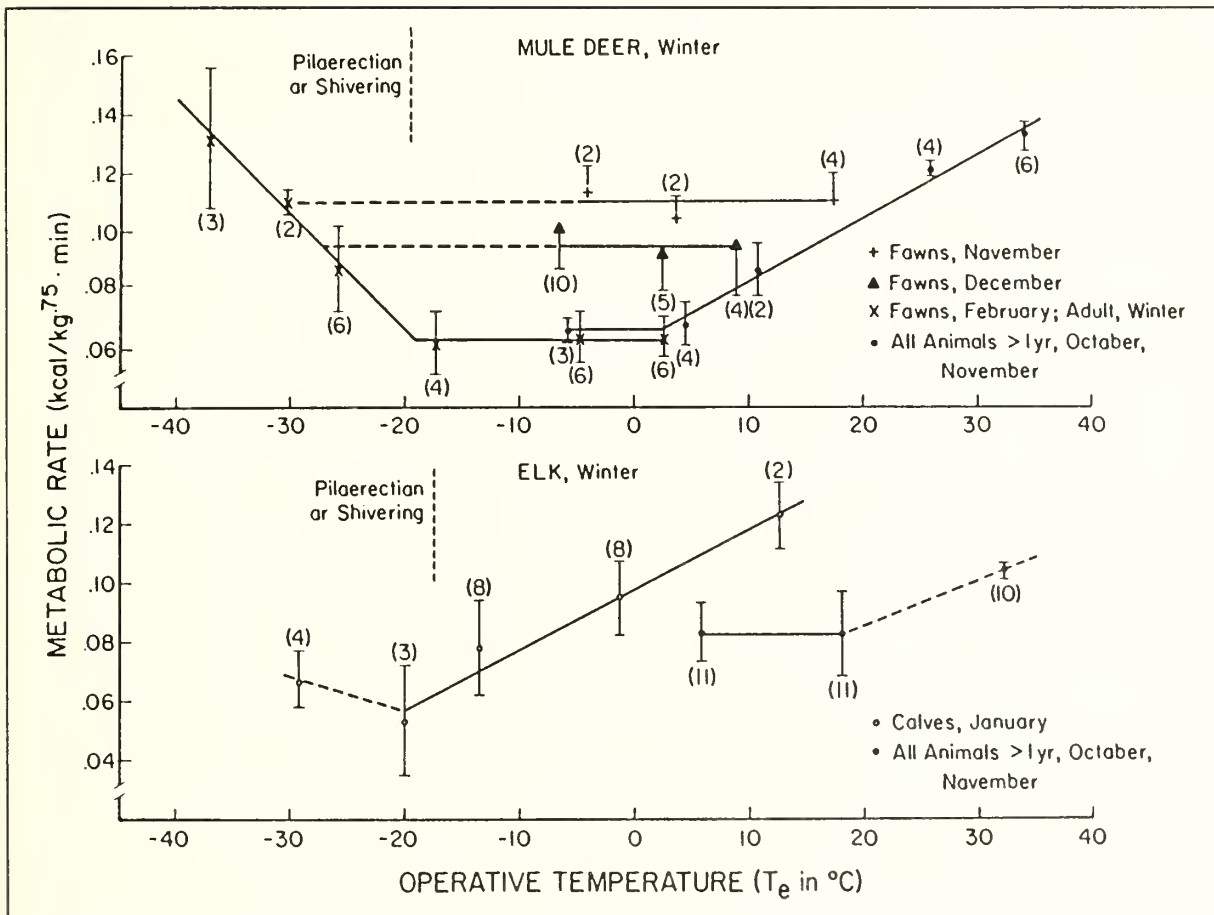


Figure 26—Energy expenditure of standing in winter as a function of operative temperature for mule deer and elk. Values in parentheses are number of samples (from Parker and Robbins 1984).

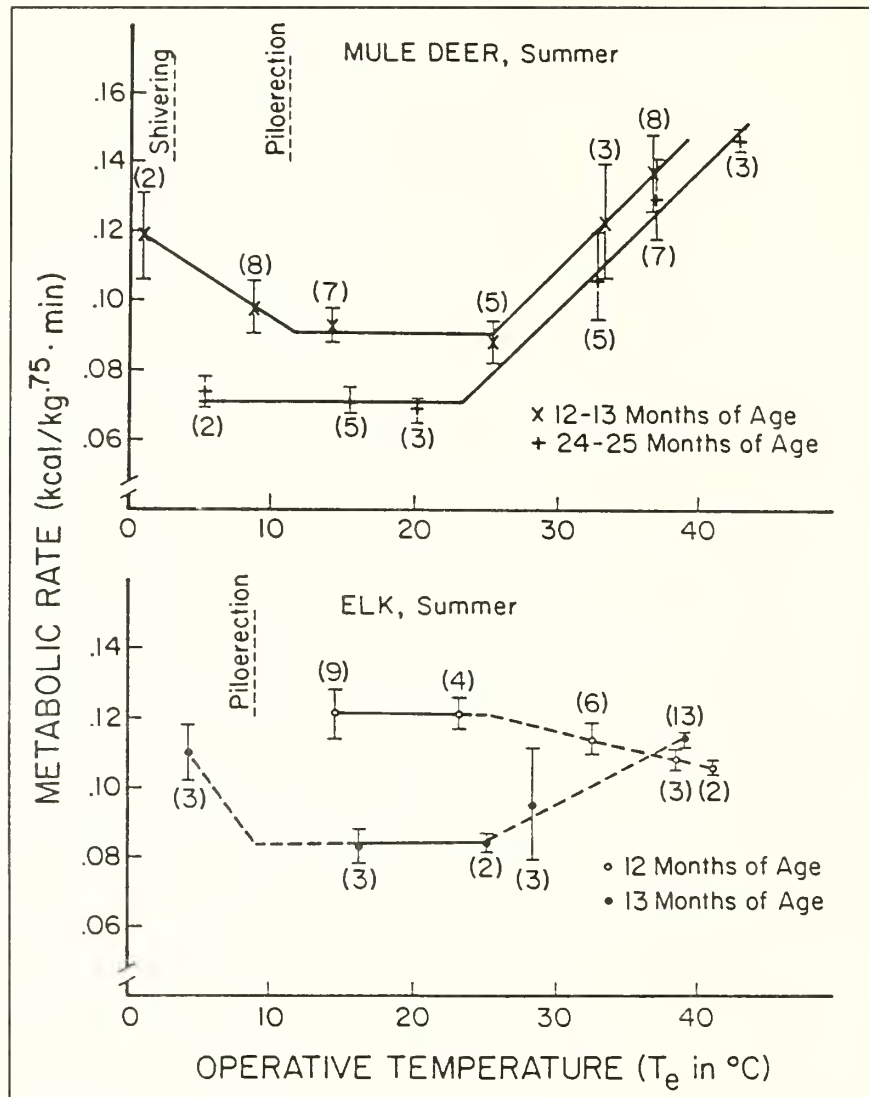


Figure 27—Energy expenditure of standing in summer as a function of operative temperature for mule deer and elk. Values in parentheses are number of samples (from Parker and Robbins 1984).

Foraging Efficiency

Because foraging efficiency is the product of many interacting factors, a model of the process is necessary if we are to understand the relative importance of individual factors. Wickstrom and others (1984) developed such a model (fig. 28) to evaluate the effects of forage biomass and diet dry-matter digestibility (fig. 29), baseline energy requirements (fig. 30), and snow depth (fig. 31) with all other factors held constant. The model calculated the grazing time required for an animal to meet its daily energy costs. High foraging efficiency corresponded to low required grazing time.

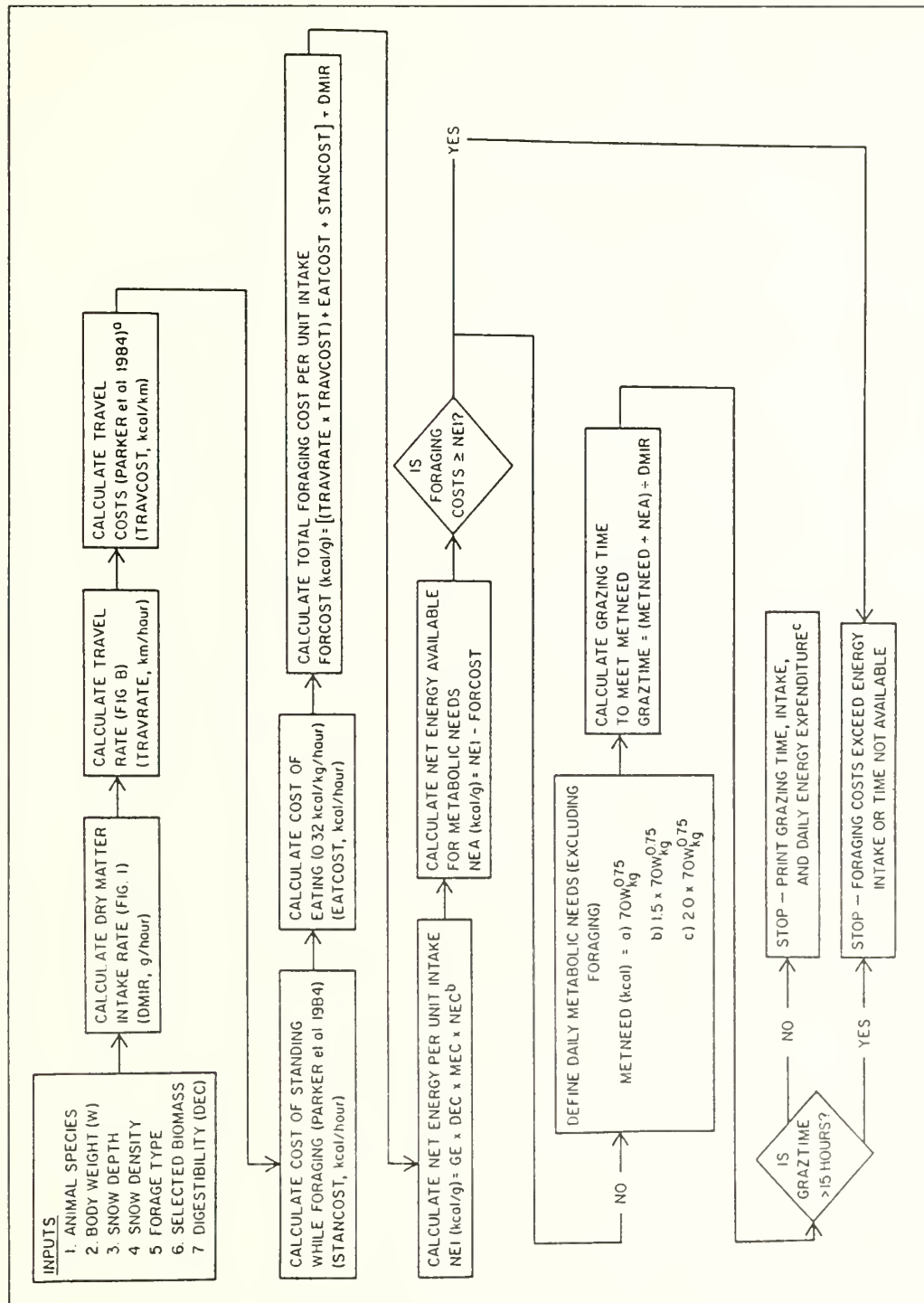


Figure 28—Foraging energetics model (from Wickstrom and others 1984). Simulation was based on the following assumptions: (1) travel cost with and without snow was calculated for horizontal locomotion only; (2) net energy intake was calculated using 4.4 kcal/g as the forage gross energy (GE) content, 0.82 as the metabolizable energy coefficient (MEC), and 0.70 as the net energy coefficient (NEC); and (3) foraging was limited only by time, with no physical constraints on digestive tract capacity.

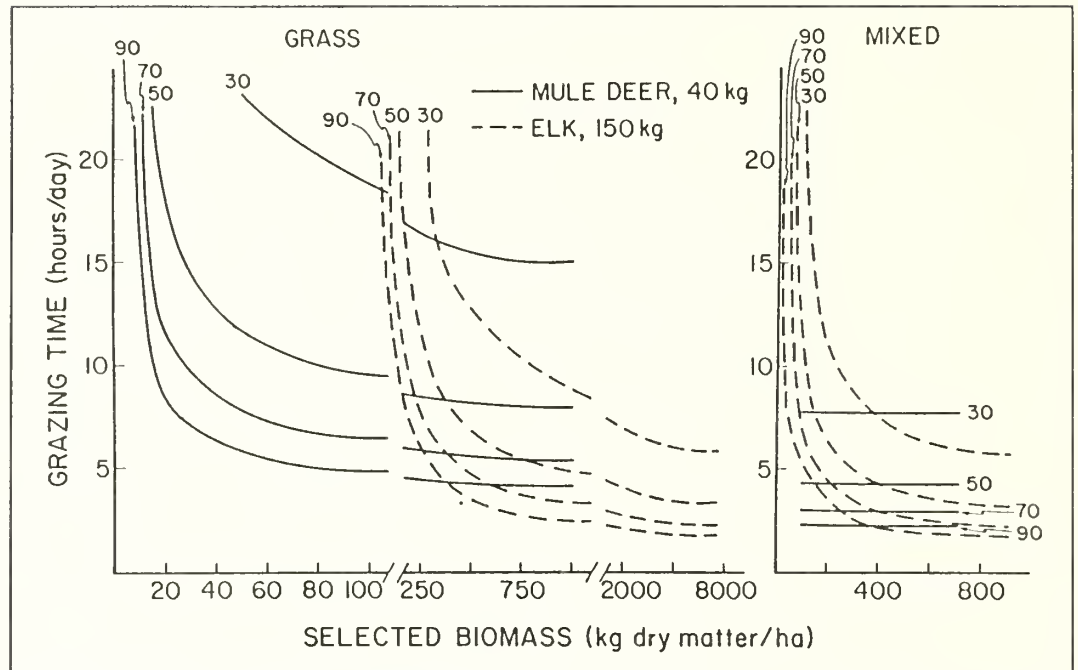


Figure 29—The effect of variation in forage biomass and forage digestibility on the grazing time required for mule deer and elk to meet minimum maintenance energy requirements (basal metabolism and foraging activity costs, excluding thermoregulation) in grass and mixed communities. Differences in forage quality were simulated by varying the digestible energy coefficient from 30 to 90 percent (from Wickstrom and others 1984).

Grazing time required to meet minimum energy requirements decreased curvilinearly with increasing forage availability in grass and mixed understory communities (fig. 29). Because of the asymptotic relation between forage biomass and dry-matter intake rates (fig. 17), forage biomass affected foraging efficiency only at low levels for deer but higher levels for elk. Variation in diet digestibility, on the other hand, had a major effect on both the slope and inflection point of the curves relating grazing time to biomass for both deer and elk in both types of habitat (fig. 29). The inflection points shifted toward greater forage biomass as digestibility decreased, especially toward the lower end of the range of digestibilities. Precise estimates of diet digestibility, therefore, are most important at the lower range of digestibilities: A drop from 50 to 30 percent is much more significant than is a drop from 90 to 70 percent.

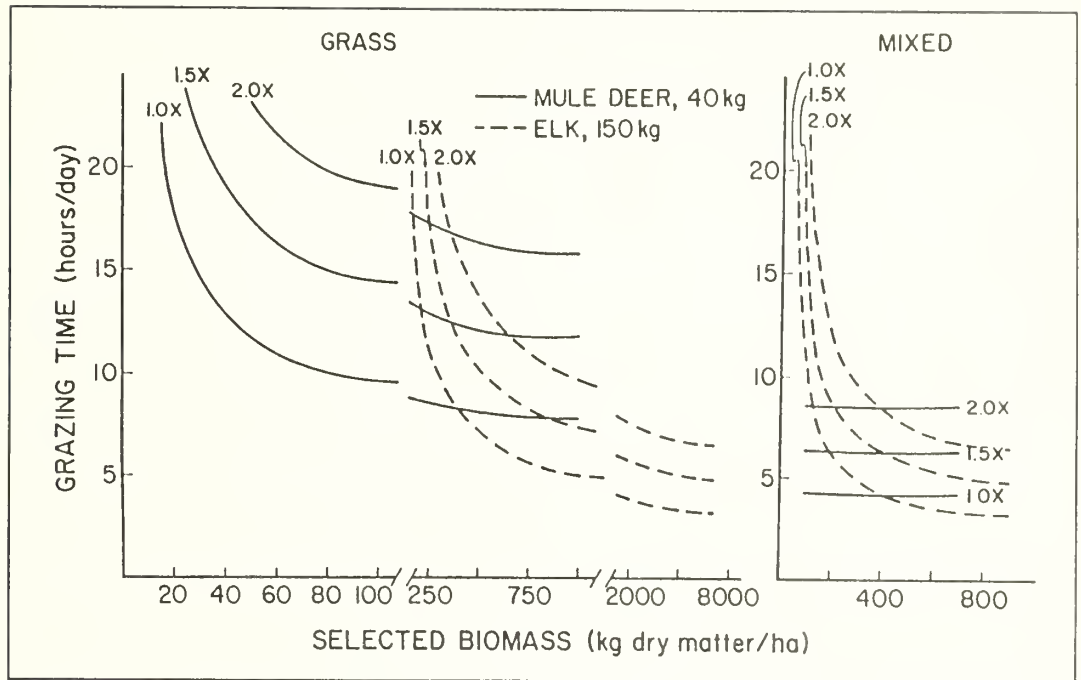


Figure 30—The effect of differing levels of baseline energy metabolism as increments of basal metabolic rate on requisite grazing times of mule deer and elk in grass and mixed communities. Calculations were based on a constant digestible energy coefficient of 50 percent (from Wickstrom and others 1984).

Elk must spend less time than mule deer to meet energy needs when consuming grass of equivalent biomass (except at low forage biomass) and digestibility (fig. 29). When foraging in mixed communities, however, the deer's greater intake per unit of metabolic weight enabled it to meet its requirements within the same timeframe as the elk. This is consistent with the general observation that graminoids constitute a more important element of elk diets and habitats than those of deer (Hanley 1984a). The disparity between deer and elk in foraging efficiency decreased when diet digestibility was high, indicating the relative importance of a high-quality diet to the smaller deer. It was much more unprofitable for elk than deer to graze in communities of low biomass, however, indicating the relative importance of forage biomass to the much larger elk.

Grazing time required to meet energy needs increased with increases in the animal's baseline energy metabolism (fig. 30). Changes in baseline energy requirements, as might result from seasonal changes in basal metabolic rate or thermoregulatory costs, had a greater absolute effect on deer than on elk in grass communities because of the lower foraging efficiency of deer in grass habitats.

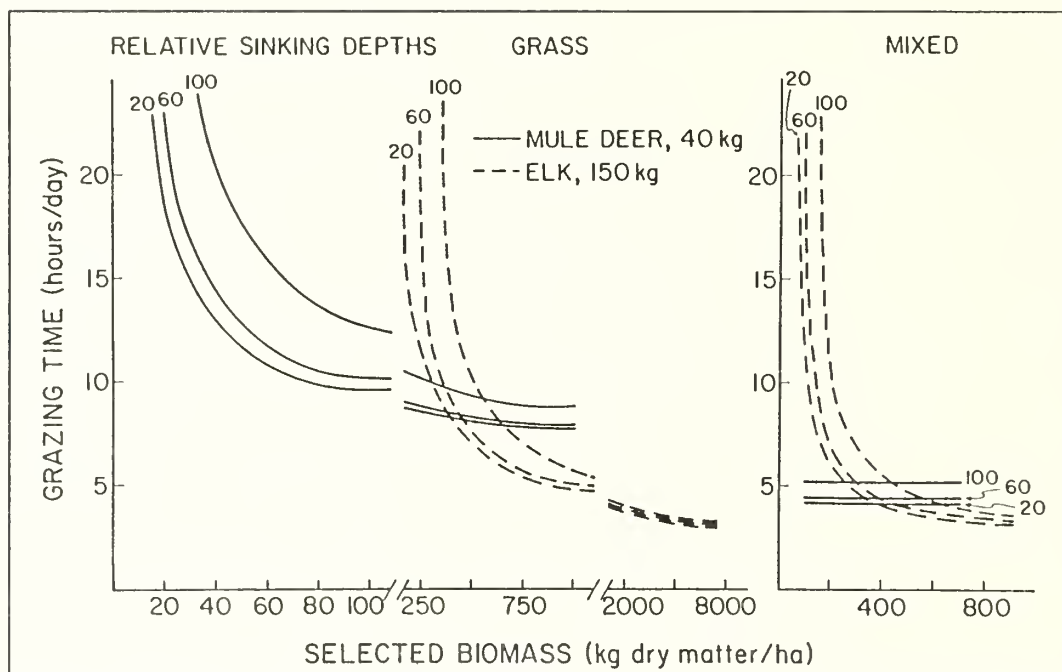


Figure 31—The effect of differing snow depths on requisite grazing times of mule deer and elk in grass and mixed communities. Snow was assumed to affect only travel costs. Relative sinking depths were calculated as a percentage of brisket height. Corresponding snow depths for the deer were 10.6, 31.9, and 53.1 cm. Equivalent elk values were 14.9, 44.8, and 74.7 cm. Calculations were based on a constant snow density of 0.3 g/cm^3 , forage digestibility of 50 percent, and minimum baseline energy metabolism of 1.0 times basal metabolic rate (from Wickstrom and others 1984).

Because snow increased the activity cost of foraging, grazing time required to meet minimum energy needs increased with the depth to which the animal sank (fig. 31). The increment in necessary grazing time was small as long as forage biomass was great enough to permit asymptotic rates of intake. At low levels of biomass, however, traveling distance increased and required grazing time increased dramatically. The most important effect of snow, therefore, is how it affects forage availability and, particularly, diet quality. The 20 cm of snow responsible for shifting the estimated diet digestibility from 58 to 38 percent in figure 16A would have major effects on the energy intake side of foraging efficiency but relatively minor effects on the energy expenditure side. At moderate to deep levels of snow, however, when much forage is already buried, the effects on energy expenditure become more important, especially at sinking depths near or greater than brisket height.

This analysis of foraging efficiency is only the beginning of what is needed for understanding the importance of various environmental factors to deer. The model needs to be expanded to include the interaction between rumen turnover rate and diet digestibility (Spalinger and others 1986) and the behavior of deer in terms of diet selection, habitat selection, and activity budgets. Energy acquisition is of fundamental importance to deer, but the intake of adequate levels of digestible protein also may be a problem in some habitats. And until we understand the nutritional basis of habitat selection by deer, we will have difficulty extrapolating our knowledge of foraging efficiency to deer behavior and estimates of carrying capacity. In the meantime, however, many new implications for forest management have emerged and will continue to emerge.

Management Implications

The principal ecological effect of timber management is to alter the disturbance regime of the forest overstory. This in turn affects the environment and dynamics of understory vegetation and the characteristics of habitat for wildlife. Historically, the disturbance regime of most of the forests of southeastern Alaska has been one of high-frequency, low-magnitude disturbance with individual trees or small groups of trees dying or being blown down by wind and gap succession predominating. When forests are clearcut, the disturbance regime is changed to one of low-frequency, high-magnitude disturbance with succession occurring as even-aged pulses. The understory environment varies greatly from place to place and from time to time with gap succession. But when succession proceeds in even-aged pulses, the spatial heterogeneity is greatly reduced and the understory environment becomes much more uniform. This shift in disturbance regime has major consequences for both plants (Brady and Hanley 1984) and animals (Hanley and others, in press).

Other factors than vegetation also influence animal population densities. Weather, of course, has major effects on food availability and foraging efficiency of deer as snow buries vegetation and increases energy costs of locomotion. Deer also affect their food supplies in a density-dependent fashion. Overbrowsing decreases the production of preferred foods and changes the species composition of plant communities. Wolves, too, influence deer populations. When wolf densities are high and deer densities are low, wolves probably exert a major influence on populations of deer. More important than deer and wolf densities alone, however, is their relation to the reproductive rate of the deer (Van Ballenberghe and Hanley 1984). Highly productive deer herds can sustain much higher levels of predation than can herds with low productivity (fig. 32). Deer productivity, of course, depends on the nutritional status of deer, which mainly depends on the productive capacity of the habitat. Forest management affects the balance between deer and wolves by changing the quantity and quality of food resources for deer and the effects of forest overstory on snow interception.

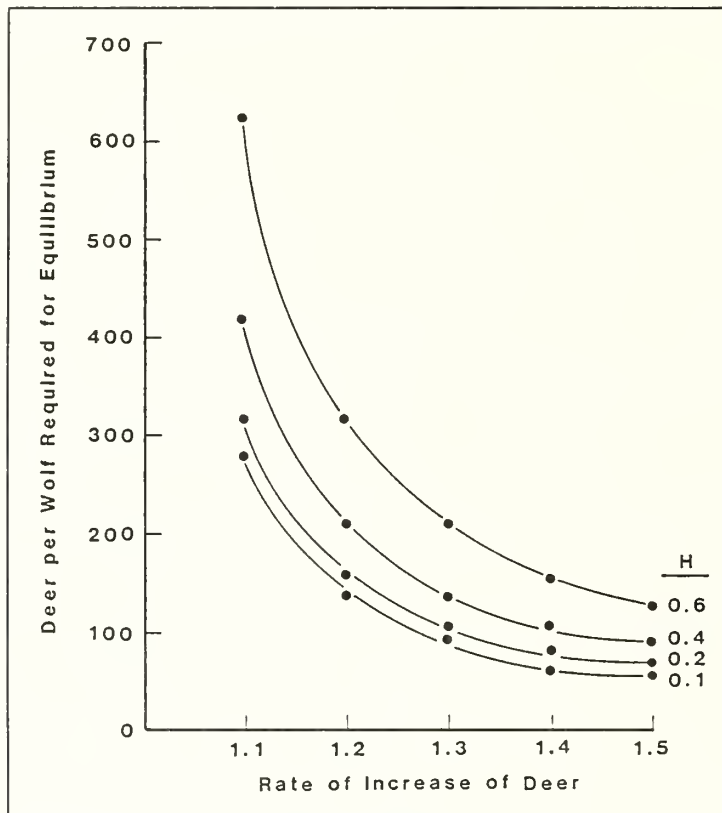


Figure 32—Relations between deer:wolf ratios required for deer population equilibrium and annual rate of increase of deer at various hunting intensities (H). Predation rates are constant at 25 deer killed per wolf per year. H is the proportion of annual increment of deer removed by hunting (from Van Ballenberghe and Hanley 1984).

Old-growth forests are an especially important habitat for Sitka black-tailed deer because they provide a rich and diverse mix of high-quality food resources that remain relatively available even during periods of snow accumulation. Shaded (low-tannin, high-protein) leaves are important in summer; and evergreen herbs, lichens, and snow interception are important in winter. The importance of old-growth forests is not unique to Sitka black-tailed deer. Where understory productivity in even-aged stands is low or where snow accumulations are deep, old-growth forests are critical habitat for Columbian black-tailed deer, Roosevelt elk, and woodland caribou for virtually the same reasons as for Sitka black-tailed deer (Hanley and others 1984). But the question of whether old-growth forest is a "habitat requirement" has no simple or general answer. The answer depends on the degree to which old-growth and even-aged forests differ in their ability to meet the behavioral and physiological requirements of deer, as well as the degree to which those requirements can be satisfied in the absence of old growth. What constitutes a habitat requirement also depends on the population density and productivity desired by management. Where lower levels of productivity are desired, habitat requirements are less stringent. These determinations must be made on a case-by-case basis and be based on a rather detailed understanding of factors limiting the particular population (Hanley and others 1984).

It is important to keep in mind that much variation exists in the general patterns of overstory-understory and overstory-snow relations discussed in the beginning of this report. Both old-growth and even-aged forests are highly variable in their structure, species composition, and productivity. Many exceptions to the general patterns exist (note the high degree of variation evident in figures 2-7). Therefore, it is especially important that forest managers and biologists become familiar with the particular land under consideration and that they understand the ecological relations between deer and their habitat, so they can make informed judgments on a case-by-case basis. The greatest management implication of the work reviewed here is its contribution toward furthering our understanding of deer ecology. General "rules of thumb" are few and must be weighed carefully.

What is needed for effectively managing both timber and habitat resources simultaneously is a means of quantitatively evaluating habitat for deer and a program of management that protects important old-growth stands and enhances even-aged stands.

Habitat Evaluation

The relative values of habitats differ depending on whether one is interested in the value of habitat to an individual animal (as in foraging efficiency and habitat preference) or to a population of animals (as in carrying capacity). Carrying capacity can be defined as the maximum density of animals that can be supported by a given habitat. Obviously, carrying capacity must vary with the specified age, sex, body weight, and reproductive status of the animals because these factors determine the nutritional requirements of the population. Also, because habitats are constantly changing (seasonally and with succession), carrying capacity constantly changes. Carrying capacity, therefore, is a theoretical concept only. Its practical utility is in providing a quantitative measure of the productive capacity of a habitat for animals under a specified set of circumstances. It has meaning only in the context of specified animal requirements and specified forage resources.

Both the availability and nutritional quality of forage are important determinants of both foraging efficiency and carrying capacity, and foraging efficiency and carrying capacity are interrelated. The relative importance of forage availability and quality, however, are very different for foraging efficiency and carrying capacity. For foraging efficiency, concentration of digestible energy in the food is much more important than food biomass at all but very low levels of biomass for deer (<25 kg/ha). For carrying capacity, on the other hand, food biomass is obviously of very great importance as long as it is at least of a minimum quality that meets the nutritional requirements of the deer.

The major reason for these differences is that although carrying capacity is essentially a linear function of acceptable biomass (the quantity of food divided by the intake per deer), dry-matter intake rate of a foraging deer is an asymptotic function of biomass. The key to understanding the interplay between foraging efficiency and carrying capacity is that above a minimum threshold of food biomass, nutritional quality is the most important factor affecting foraging efficiency; above minimum thresholds of foraging efficiency and nutrient intake, however, food biomass determines carrying capacity (Hanley and others, in press). Habitats with high foraging efficiency do not necessarily have high carrying capacity (for example, high quality but low quantity of food), and habitats with high carrying capacity do not necessarily have high foraging efficiency (for example, high quantity but only minimally acceptable quality of food). If habitat selection by individual deer is based primarily on foraging efficiency, therefore, habitat preferences may have little relation to carrying capacity.

Hanley and Rogers (1989) have provided a method of estimating carrying capacity based on the quantity of available forage meeting specified nutritional constraints. The constraints are for minimum concentrations of digestible energy and digestible protein, specified on the basis of the nutritional requirements of the animals. Two additional constraints are that no single forage can constitute more than 40 percent of the diet and that only total biomass greater than 25 kg/ha is available for consumption. The method enables one to calculate carrying capacity (deer days per hectare) for a specified listing of plant species, their biomass and concentrations of digestible energy and digestible protein, and nutritional requirements of the deer (daily dry-matter intake and minimum dietary concentrations of digestible energy and digestible protein).

Hanley and Rogers (1989) used the procedure to estimate carrying capacity of four hypothetical habitats during summer and during winter with three different snow depths and for two levels of nutritional requirements of adult does. The results (fig. 33) illustrated the importance of specifying the environment and nutritional requirements of the animals. Depending on time of year, snow depths, and nutritional status of the deer, the relative carrying capacities of the four habitats were very different.

Estimates of carrying capacity based on nutrition provide a theoretical maximum estimate of carrying capacity—the density of deer that could be supported by the habitat *if* deer choose to make maximum use of the habitat. The additional factor of habitat choice by animals is an important one because there may be features of the habitat that make it unattractive to deer and therefore of lower suitability. For example, habitats adjacent to busy roads and centers of human activity are likely to receive less use than are similar but remote habitats, especially during hunting season. Habitats with a variety of hiding cover and vantage points (such as ridges and knolls) are generally preferred over more uniform habitats. The variety of habitats and distance between them also are important if deer are to make maximum use of the best habitats as their relative qualities change from time to time. The concepts of home range and established patterns of use also are very important: Deer are creatures of habit as well as habitat. Areas with traditionally heavy use by deer should receive special emphasis in habitat evaluations. Nutritionally based estimates

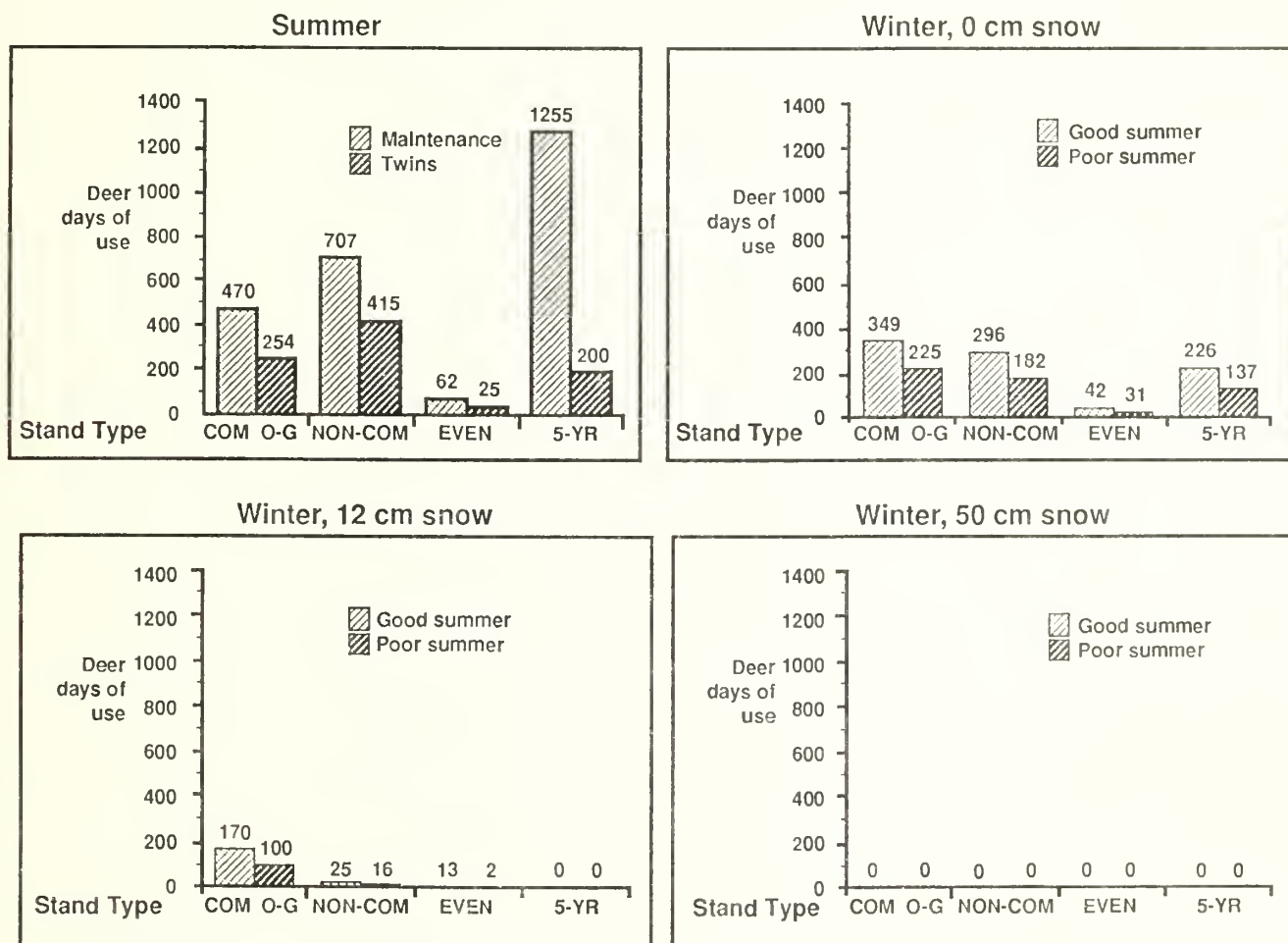


Figure 33—Estimated carrying capacities (deer days of use by adult does) of four habitats during summer and winter with three mean snow depths in the open and two levels of metabolic requirements of the deer (from Hanley and Rogers 1989). Values are calculated on the assumption that stated conditions remain constant throughout the entire season. For variable winter weather, carrying capacities must be calculated on the basis of mean forage availabilities over the entire winter. COM O-G = commercial old-growth stand; NON-COM = noncommercial old-growth stand; EVEN = closed-canopy, even-aged stand; 5-YR = 5-year-old clearcutting; Good and poor summer refer to the quality of the summer range preceding use of the winter range.

of carrying capacity, therefore, must be tempered in the habitat evaluation process by consideration of other factors affecting deer behavior as well. Those factors, however, are beyond the scope of this report.

Habitat Protection

Habitat protection is currently the most important aspect of habitat planning for deer in southeastern Alaska. The emphasis has been on minimizing winter mortality of deer, and the focus has been on the importance of low-elevation, old-growth forests as critical winter range. Such habitats are especially important in areas where summer range is not of sufficient quality for high reproductive rates of deer, where wolves coexist with deer, or where winter snow accumulations are frequent and persistent because each of these factors acts to reduce the rate of population increase below that of which deer are biologically capable. In the absence of these three factors, however, critical winter range is less important, because deer herds could be expected to recover rapidly after an occasional severe winter. Criteria for critical winter range have been reviewed by Hanley (1984b) and Hanley and Rose (1987) and emphasize topography where snow accumulations are minimal, overstory canopy coverage (>95 percent, measured with a spherical densiometer) and net timber volume (>20,000 board feet per acre) sufficient for intercepting significant amounts of snow, and species composition and production of the understory sufficient for providing a high-quality winter diet. Dry-matter digestibility of the diet is an especially important factor, and evergreen herbs, lichens, and cedar foliage are especially important foods. Blueberry twigs also are an important food source but, alone, are not sufficient to meet the energy requirements of deer.

Although winter range is important, our research indicates greater attention should be given to summer range than has been the case in the past. The quality of summer range has a major influence on the reproductive rate of deer and the body reserves of deer entering winter. Deer in extensively clearcut habitats may have difficulty meeting protein requirements for lactation if they must rely heavily on open clearcuts for feeding areas because tannin concentrations are high in sun-grown leaves. Non-commercial stands could play an important role in the nitrogen economy of deer in such a situation by providing habitats with shade-grown (low tannin) leaves. But more important than summer range per se is the relation between the carrying capacities of summer and winter ranges. The population will be limited by whichever carrying capacity is lowest. Therefore, winter ranges for deer coming from highly productive summer ranges should receive priority over other winter ranges. Similarly, summer ranges for deer coming from high-quality winter ranges should receive priority over other summer ranges. Subalpine habitats with a rich supply of succulent forbs are especially valuable summer habitats. Winter ranges providing a diverse mix of habitats are especially valuable winter ranges.

Spring is a transitional period but is an especially important time of the year for both winter mortality and reproduction. By spring, deer are in their poorest body condition of the entire year, and for does, gestation requirements are becoming significant. The timing of spring, therefore, is very important to deer. Skunkcabbage is an especially important forage species in spring, with very high dry-matter digestibility (about 87 percent; Hanley and McKendrick 1983) and crude protein concentration (about 50 percent; Hanley and McKendrick 1983). It is avidly sought by deer, especially when it is the first forage initiating spring growth. Low-elevation, snow-free forests with much skunkcabbage are very important at this brief but significant time of year. Although noncommercial stands frequently have understories dominated by skunkcabbage, they may contain appreciable amounts of snow in spring. Special attention, therefore, should be given to low-elevation, commercial forests (>20,000 board feet per acre, net volume, and >95 percent crown closure) with blueberry/skunkcabbage understories for their importance in spring, especially where snow accumulations are common.

In southeastern Alaska, Admiralty Island probably typifies the ideal combination of extensive, highly productive subalpine summer ranges and extensive winter ranges of a great diversity of habitats with high carrying capacities. Admiralty Island is also free from wolves. The combination of highly productive summer ranges, extensive variety of winter and spring habitats including critical winter ranges of old-growth forest, and lack of wolves should result in very resilient deer herds capable of recovering rapidly from occasional severe winters. The greatest long-term threat to deer on Admiralty Island probably is overgrazing by the deer themselves.

Until more is known about silvicultural manipulations and other methods of habitat enhancement in even-aged stands, habitat protection will continue to be the key factor in habitat management for deer in southeastern Alaska. Careful attention should be given to the selection of old-growth retention areas within the managed forest.

Habitat Enhancement

Clearcut logging of old-growth forests in southeastern Alaska has four effects that act to decrease carrying capacity of habitat for deer: (1) sun-grown plants in open clearcuts have lower digestible protein concentrations than do shade-grown plants in forests; (2) large amounts of logging slash increase energy costs of locomotion for deer and reduce the area of usable habitat; (3) snow accumulates and persists to a much greater degree in open clearcuts than in forests; and (4) understory production is reduced to extremely low levels when the conifer canopy closes at about age 20 to 30 years and remains extremely low for at least the next 100 years. Clearcuts have one effect that acts to increase carrying capacity: Understory production is extremely great during the first 20 to 30 years of age.

The net effect on foraging efficiency and carrying capacity depends on circumstances. In most cases, foraging efficiency probably will be decreased unless the old-growth habitats have been overgrazed and high-quality food plants are scarce, or new, high-quality species become established in the clearcuts. The increase in biomass alone, above asymptotic levels of intake, will not improve conditions for individual deer. A net gain in forage biomass, however, may increase carrying capacity as long as the forage is of sufficient quality to meet the nutritional requirements of deer.

Such an increase in carrying capacity would be greatest during the initial years after logging and would decrease as increasingly greater proportions of the landscape become closed-canopy, even-aged forest. The challenge to forest managers, therefore, is in decreasing the negative effects and increasing the positive effect of logging.

Precommercial thinning is likely to yield only very limited benefits, primarily providing an extra 5 to maybe 10 years of useful life of clearcuts for deer. The problem is that shrubs, and in many cases hemlock seedlings, dominate the site and shade out the herbs. The rich diversity of forages in most old-growth stands results from the high-frequency, low-magnitude disturbance regime that characterizes old-growth stands and maintains a constant mix of environments within the understory. Any system of even-aged management will create a regime of low-frequency, high-magnitude disturbance, with the consequence of making the understory environment relatively uniform and the resulting vegetation dominated by one or a few of the most competitive and already dominant species. Despite the great biomass of shrubs and hemlock, carrying capacity will be limited by the availability of forbs. Shrubs and hemlock alone do not provide a nutritionally adequate diet in either summer or winter. In the future, as closed-canopy, even-aged stands with depauperate understories are clearcut, however, understory dynamics may be very different than those following clearcutting of old-growth stands (Brady and Hanley 1984). Adventitious herbs may become much more common and shrubs much less dominant as plants must seed into the site rather than simply be released from light interception by the overstory. The ever-present hemlock seedlings in the duff of even-aged stands, however, may respond quickly to release from light interception.

Fertilization of young clearcuts, especially with nitrogen, may decrease the ratio of carbon to nutrients in plants and increase the concentration of digestible protein in their leaves. But it also would likely increase the production of shrubs and conifers and shorten the time before canopy closure. Fertilization has been studied very little in southeastern Alaska, so quantitative guidelines are not available. It may provide a means, however, of increasing forage quality in clearcuts at the expense of their useful life-expectancy for deer. Its benefits would be very limited but in some situations could be important.

Logging slash is often very dense. And precommercial thinning increases it. Slash densities in southeastern Alaska are usually considerably greater than those modeled by Parker and others (1984) and probably are a major factor affecting use of clearcuts by deer. Slash can be reduced mechanically or manually by removal and piling. Or it can be burned. Burning with a "hot" fire is a very effective means of reducing slash.

Burning young clearcuts also offers another potentially major benefit: It reduces shrub and conifer biomass and increases the diversity of forage plants. Controlled burns have seldom been conducted in southeastern Alaska. Unpublished observations at three burned sites (Freshwater Bay, Sitkoh Lake, and Kake), however, indicate a major reduction in the dominance of blueberry and other shrubs, increased species richness and production of forbs, and greatly reduced densities of slash. Chemical composition of understory species does not appear to be affected by burning (Van Horne and others 1988), but diet quality may differ greatly from that in unburned clearcuts, depending on the differences in species composition of the habitats. Burning also may extend the period of time before conifer canopy closure. The potential effects of fire as a management tool is an area of needed research in southeastern Alaska.

Not much can be done about snow interception in young stands. Opening the canopy of older stands to maintain an understory will decrease their interception of snow as well. On winter ranges where snow is a problem, even-aged stands present a major problem for deer. Forage is likely to be most available under the forest canopy near the edges of openings in the forest. Forest edge, therefore, may in this sense be an important component in habitat management for deer. Small openings and gaps within the closed-canopy, even-aged stands could be especially valuable. But old-growth habitat protected as critical winter range will be most valuable during periods of snow.

In any case, management of even-aged stands for deer habitat must be planned on a long-term basis to provide a continuous mix of open clearcuts and forests. Small clearcuts and a mixture of many different ages are desirable for maintaining the combination of open clearcuts and forests within the home ranges of deer (Hanley 1984b). Noncommercial old-growth stands and commercial stands retained for habitat protection are additional important components of habitat diversity.

Research Needs

The research reviewed here has concentrated on forest habitats and the nutritional ecology of deer. Vegetation, snow, plant chemical composition, and deer physiology and nutritional requirements have been emphasized. Together, these provide a nutritional basis for estimating carrying capacity and understanding the important features of habitat for deer. But their relation to deer behavior, particularly food and habitat selection, remains mostly hypothetical. In the end, it really does not matter how good a habitat *should* be if it is not used by deer. The contribution of habitats to the carrying capacities of landscapes depends on both their nutritional value and their use by deer. The preceding analyses provide several important hypotheses about the nutritional basis of habitat selection by deer, the most important of which is that habitat selection is closely related to foraging efficiency. That hypothesis must be tested if we are to really understand the most important factors of habitat for deer.

Although significant progress has been made in recent years in understanding the role of tannins in dietary quality of deer, more work is needed to understand their role in toxicity and the diet selection process. We also need to further test our equations for estimating digestibility of protein and dry matter. And we need to more clearly understand the relations between environment (including herbivory) and plant production and chemistry, especially phenolic chemistry.

Several areas of vegetation management stand out as being in particular need of study: (1) identification of palatable forages containing highest concentrations of digestible protein in sun-grown leaves; (2) how to encourage their growth and the growth of forbs in clearcuts; (3) the potential role of fire and fertilization in improving the quality of clearcuts for deer during snow-free conditions; (4) how to increase production of forbs, especially evergreen forbs, in even-aged stands; and (5) the potential role of silviculturally created gaps in providing available forage in even-aged stands during periods of snow.

Additionally, further study must be directed at landscape-level evaluations of patch dynamics and long-term planning of habitat management for deer.

Common and Scientific Names

Common name	Scientific name
Animals:	
Columbian black-tailed deer	<i>Odocoileus hemionus columbianus</i> (Richardson)
Elk	<i>Cervus elaphus</i> Linnaeus
Gray wolf	<i>Canis lupus</i> Linnaeus
Mule and black-tailed deer	<i>Odocoileus hemionus</i> (Rafinesque)
Roosevelt elk	<i>Cervus elaphus roosevelti</i> (Merriam)
Sitka black-tailed deer	<i>Odocoileus hemionus sitkensis</i> (Merriam)
White-tailed deer	<i>Odocoileus virginianus</i> (Zimmermann)
Woodland caribou	<i>Rangifer tarandus caribou</i> (Gmelin)
Plants: ²	
Alaska blueberry	<i>Vaccinium alaskensis</i> How.
Alaska yellow-cedar	<i>Chamaecyparis nootkatensis</i> (D. Don) Spach
Alder	<i>Alnus</i> spp. Mill.
Beard lichen	<i>Alectoria sarmentosa</i> Ach. and <i>Usnea</i> spp. (Dill.) Adans.
Blueberry	<i>Vaccinium</i> spp. L.
Bunchberry dogwood	<i>Cornus canadensis</i> L.
Deerberry	<i>Maianthemum dilatatum</i> (How.) Nels. & Macbr.
Deer cabbage	<i>Fauria crista-galli</i> (Menzies) Makino
Deer fern	<i>Blechnum spicant</i> (L.) Roth
Devilscub	<i>Oplopanax horridus</i> (Sm.) Miq.
Feathermoss	<i>Hylocomium splendens</i> (Hedw.) B.S.G.; <i>Rhytidiadelphus loreus</i> (Hedw.) Warnst.

² Plant names are from Hultén (1968).

Foamflower	<i>Tiarella trifoliata</i> L.
Golden menziesia	<i>Menziesia ferruginea</i> Sm.
Goldthread	<i>Coptis aspleniifolia</i> Salisb.
Hairgrass	<i>Deschampsia caespitosa</i> (L.) Beauv.
Labrador tea	<i>Ledum palustre</i> L.
Lady fern	<i>Athyrium filix-femina</i> (L.) Roth
Lobaria	<i>Lobaria</i> spp. Schreb.
Mountain hemlock	<i>Tsuga mertensiana</i> (Bong.) Sarg
Oakfern	<i>Gymnocarpium dryopteris</i> (L.) Newm.
Rock alga	<i>Fucus furcatus</i> C. Ag.
Salal	<i>Gaultheria shallon</i> Pursh
Salmonberry	<i>Rubus spectabilis</i> Pursh
Sedge	<i>Carex</i> spp. L.
Shore pine	<i>Pinus contorta</i> Dougl. ex Loud
Sitka spruce	<i>Picea sitchensis</i> (Bong.) Carr.
Skunkcabbage	<i>Lysichiton americanum</i> Schott
Sphagnum	<i>Sphagnum</i> spp. L.
Sweet-root	<i>Osmorhiza</i> spp. Raf.
Red-berry huckleberry	<i>Vaccinium parvifolium</i> Sm.
Trailing bramble	<i>Rubus pedatus</i> Sm.
Twayblade	<i>Listera cordata</i> (L.) R. Br.
Twinflower	<i>Monesis uniflora</i> (L.) Gray
Twistedstalk	<i>Streptopus</i> spp. Michx.
Violet	<i>Viola glabella</i> Nutt
Western hemlock	<i>Tsuga heterophylla</i> (Raf.) Sarg.
Western redcedar	<i>Thuja plicata</i> D. Don
Wildrye	<i>Elymus arenarius</i> L.
Woodfern	<i>Dryopteris dilatata</i> (Hoffm.) Gray

English Equivalents

1 meter (m)	= 39.4 inches
1 centimeter (cm)	= 0.39 inch
1 kilometer (km)	= 0.53 mile
1 hectare (ha)	= 2.47 acres
1 gram (g)	= 0.035 ounce
1 kilogram (kg)	= 2.20 pounds
1 kilocalorie (kcal)	= 4186 joules = 3.97 Btu
Degrees Celsius (oC)	= 5/9 (degrees Fahrenheit - 32)

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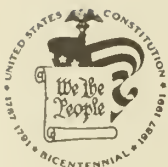
Research on forest habitats and the nutritional ecology of Sitka black-tailed deer conducted during 1981 through 1986 is reviewed and synthesized. The research approach was based on the assumption that foraging efficiency is the best single measure of habitat quality for an individual deer. Old-growth and even-aged forests differ greatly in their production of forage, protein digestibility of sun and shade-grown leaves, and relative carrying capacities for deer. Forest overstories reduce snow depths significantly, but only at high crown closures. Modeling of foraging energetics indicated that snow, even at low depths, is a critical factor affecting foraging efficiency and carrying capacity of habitats. Its greatest effect is on reducing energy intake by changing forage availability and diet composition rather than by increasing energy costs of locomotion. Foraging efficiency and carrying capacity are shown to be related but with different concepts: For black-tailed deer, forage biomass is a relatively minor factor affecting foraging efficiency but is a major factor affecting carrying capacity.

Keywords: Deer, black-tailed deer, Sitka black-tailed deer, *Odocoileus hemionus*, wildlife, habitats, forest management, Alaska, southeastern Alaska, nutrition, ecology.

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