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Relationships Between Sitka Black-Tailed Deer and Their Habitat

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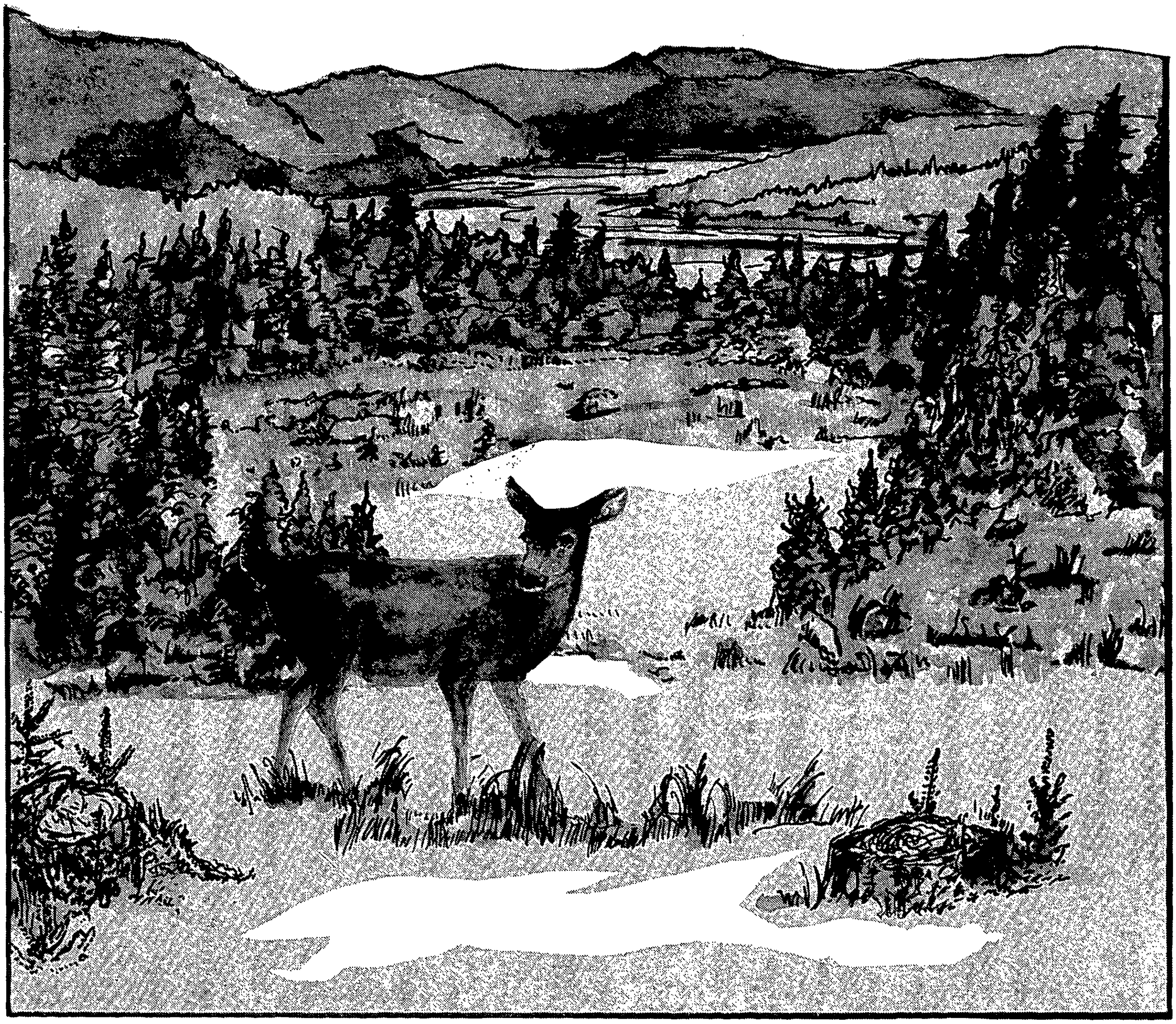

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Abstract

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Old-growth, western hemlock-Sitka spruce forest in southeastern Alaska is an important element of the habitat of Sitka black-tailed deer. The conversion of uneven-aged, old-growth forests to even-aged, second-growth forests has generated concern about the future carrying capacity of the habitat for deer, especially where snow accumulation is common on winter ranges. Even-aged, second-growth forests produce very little forage for black-tailed deer. Young (<20 years), open stands produce greater amounts of forage than do old-growth stands. Snow accumulates to greater depths in openings than in forest, however, and forage becomes unavailable to deer as it is buried in snow. Habitat quality for Sitka black-tailed deer must be viewed as an energy benefit-cost relation. Energy intake decreases and energy expenditure increases as snow depth increases. Habitats differ in their canopy characteristics and in the amount and kind of forage they produce. The relative qualities of habitats shift with changing snow conditions. An understanding of these dynamic relationships between deer and their habitat is essential for developing management objectives for deer habitat. The current theory is largely qualitative and lacks the ability to yield unambiguous, quantitative predictions. Research is needed to quantify the key relationships between forest canopy and understory production and snow interception, and between the metabolic requirements of deer and the nutritional quality of available forage.

Keywords: Wildlife habitat management, wildlife habitat, timber management, habitat selection, deer (black-tailed), Alaska (southeast).

Contents

Introduction

Sitka black-tailed deer (Odocoileus hemionus sitkensis) are endemic to the north Pacific coast from about latitude 53" to **58°** N. (Queen Charlotte Sound, British Columbia, to Icy Strait, Alaska), and occupy all of the Alexander Archipelago and a narrow strip of adjacent mainland (fig. **1).** Populations have also been established on the Queen Charlotte Islands, the Yakutat area, the islands of Prince William Sound, and Afognak and Kodiak Islands (Wallmo **1981).**

Deer harvests in Alaska are small (about 3,000 to **14,000** annually, Johnson and Wood **1979)** compared to those in most other western states, but large enough to make deer a major game species in Alaska. Deer densities on winter ranges have been estimated as high as 25 to **75** deer per square kilometer [1] (Barrett **1979).** Experienced observers believe, however, that the populations are subject to large fluctuations. Generally, declines are related to attrition from starvation during winters with deep snow and increases are related to successive open winters in which snow does not excessively restrict their range (Klein and Olson **1960,** Merriam **1968,** Olson **1979,** Reynolds **1979,** Smith **1979).**

Sitka black-tailed deer inhabit the most northwestern extension of the range of mule and black-tailed deer (Wallmo **1981).** This is a region of coastal coniferous rain forest. The maritime influence moderates temperatures, but levels of precipitation are high the year around. Historically, fires have been infrequent, and windthrow has been the major disturbance to forests (Harris and Farr **1974).** The region is characterized by uneven-aged, old-growth forest with alpine vegetation and icefields at higher elevations (commonly down to **400** m). Although temperatures are mild, compared to continental climates, the habitat of Sitka black-tailed deer has much deeper snow for longer periods than the habitat of their counterpart to the south, Columbian black-tailed deer.

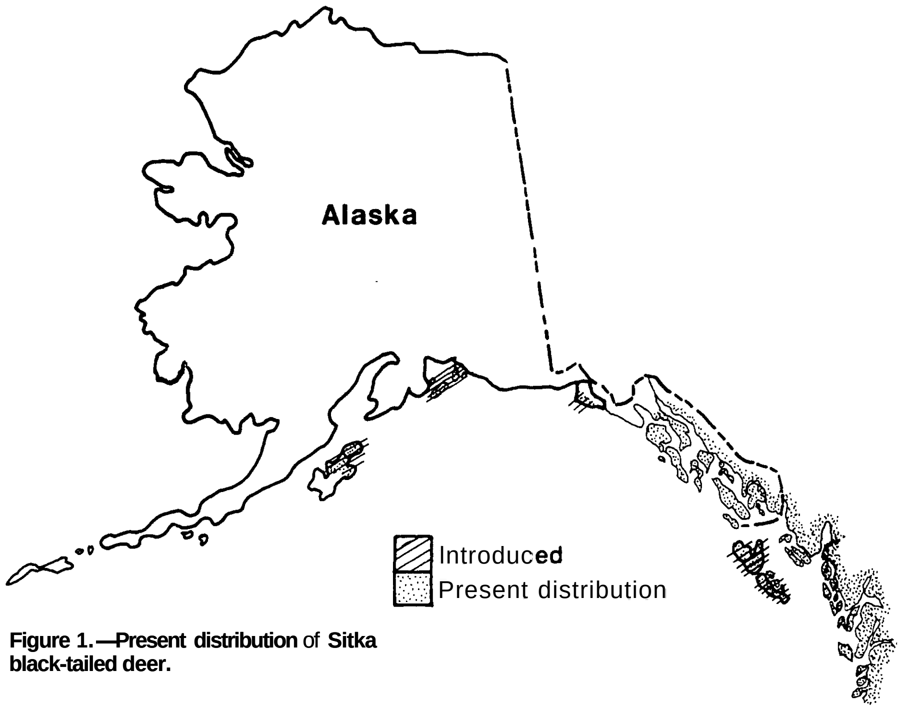

Figure 1.—Present distribution of **Sitka black-tailed deer.**

The ability of deer to survive inclement winters is influenced by their nutritional condition, the duration of forage restriction, and the amount of forage available at the end of the winter. Although subalpine habitat constitutes an important part of the summer range, the winter range is restricted to forested habitats. As snow accumulates, deer become concentrated on winter range. Management practices that alter the quality of winter range for deer have greater consequences than might be inferred from the acreages affected. This is especially true if the higher quality patches of winter range are affected.

Because logging has increased in southeastern Alaska during the past 30 years, an increasing percentage of the deer habitat will be in even-aged forest in the future. The effect of timber harvesting and stand improvement practices on the quality of habitat for deer is a major concern.

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[1] **Schoen, J. W. and Wallmo, O. C., unpublished data on file at Game Division, Alaska Department** of **Fish and Game, 230 S. Franklin St., Juneau, AK 99801.**

Nutrition and **Diet**

Energy.—The relationships between deer and their habitat are based on seasonal changes in the availability and quality of food, combined with the physiological requirements of deer. During summer, both the quantity and quality of forage are relatively high, and deer gain weight (table 1). During winter, however, both the quantity and quality of forage are low, and deer lose weight. Even in the absence of snow, deer must catabolize body reserves, principally fat and muscle tissue (Bandy and others 1970). The amount and duration of snow accumulation on the ground, however, is of critical importance to the survival of deer in winter. As snow buries forage, the quality of diet decreases along with the intake of dry matter, and energy intake decreases (table 1). At the same time, deer must spend more energy moving around as they sink deeper into snow (fig. **2).**

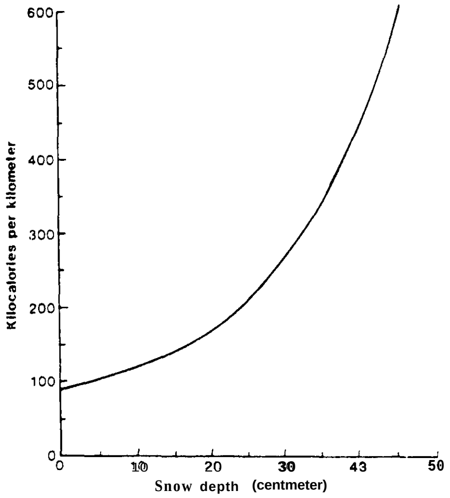

Figure 2.—Energy costs of locomotion through snow for a 40-kg deer (Source: Mattfeld 1974).

Male and female deer use energy in different ways, which is illustrated by their annual fat cycles (fig. 3). Although both males and females gain weight over the summer and lose it during the winter, the seasonal gains and losses occur earlier for males. Because of substantial weight losses during the rut in late fall, males generally begin the winter with lower fat and nutrient reserves than females (Anderson and others 1972, Fowler and others 1967, Nordan and others 1968). Adult males are especially active during the rut and spend little time foraging (Geist 1981, Nordan and others 1968). Late summer and fall is the time when females gain the most (Anderson and others 1972, Mitchell and others 1976). Forage quality and quantity are still relatively high, reproductive demands are relaxed, and energy and nutrient intake generally exceeds maintenance requirements (Short 1975). High costs of gestation and lactation (fig. **4)** usually preclude weight gain by reproductive females during spring and summer, although forage quality and quantity are at their peaks then.

Table I—Estimated daily intake of forage and energy required for maintenance of an adult black-tailed deer in summer and winter

Season	Body weight 1/	AMR 2/	Dry matter intake per kilogram$^{0.75}$ of body weight 3/	Dry matter digestibility 4/	Energy intake 5/	Net energy gain (+) or loss (-)
	Kilograms	Kilocalories	Grams	Percent	- - -Kilocalories- - -	
Summer	45	2,432	80	70	3,722	+1,290
Winter:						
Without snow	50	2,632	59	55	2,334	-298
With snow	50	2,632	48	35	1,208	-1,424

1/ Body weight for 2-yr-old doe in early summer and early winter (source: Bandy and others 1970).

2/ AMR = activity metabolic rate = c (BMR), where c is a constant that varies with seasonal activity levels, and BMR is basal metabolic rate or approximately 70 times body weight to the 0.75 power. BMR also varies seasonally. (sources: Moen 1973, Wallmo and others 1977).

3/ Ovendry weight of forage consumed per kg0.75 body weight per day (sources: Alldredge and others '9-974, Bandy and others 1970). Intake is lower during winter with or without snow.

4/ Sources: Rochelle 1980, Short 1981, Wallmo and others 1977.

5/ Energy Intake = GE de me (DMI), where GE is the gross energy content (4.5 kcal g-1), de is dry matter digestibility, me is the metabolizable energy coefficient (0.85), and DMI is dry matter intake.

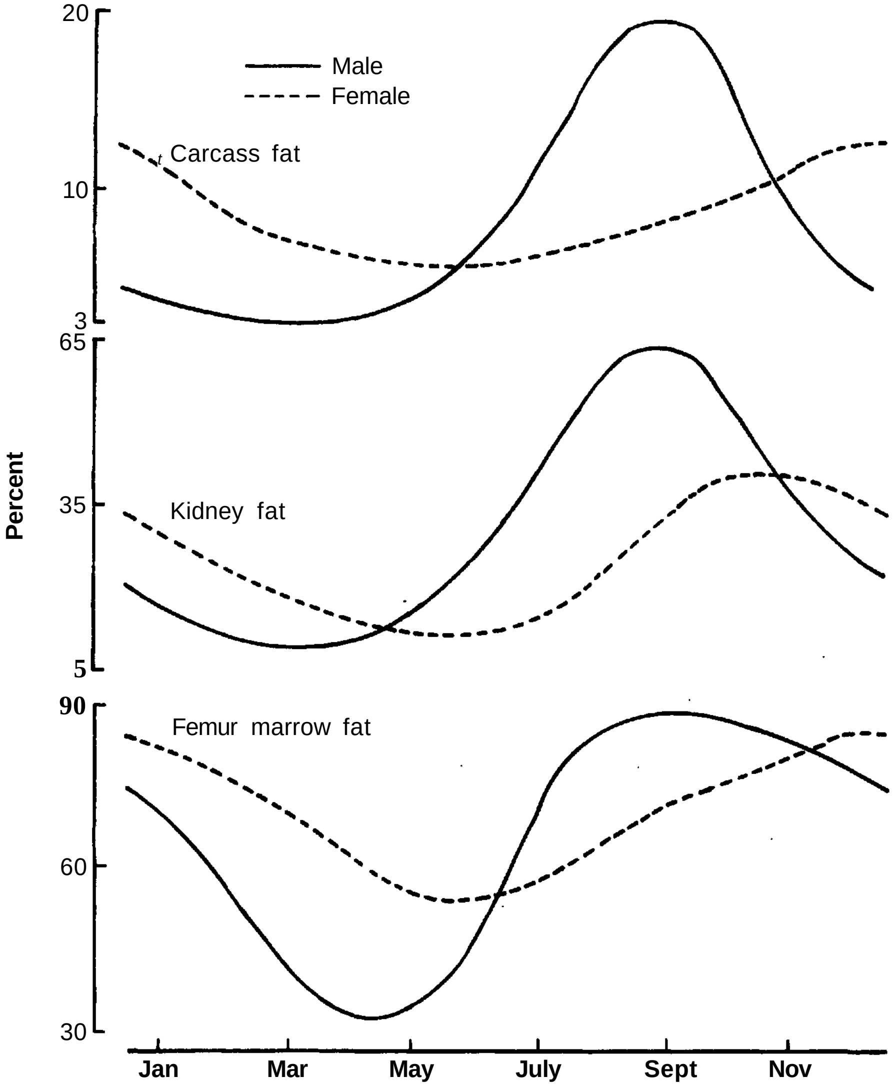

Figure 3.—Annual cycle of fat storage and depletion in mule deer (Source: Anderson and others 1972).

Reproductive costs for pregnant females are insignificant during the most severe conditions of winter. As gestation progresses through spring, however, the availability of nutritious forage is critical for successful reproduction.

Plant nutrients and secondary compounds.—Although deer have specific mineral requirements, deer-habitat relationships are understood best in terms of energy and nitrogen metabolism (Moen 1973). Energy is needed to fuel the deer, while nitrogen is needed to build body tissue. The cell-soluble portion of the forage contains most of the nitrogen and mineral nutrients, as well as readily digestible sugars, starches, and fats; the cell-wall fraction is mainly an energy source (Van Soest 1967). For black-tailed deer with a feeding strategy that emphasizes the cell-soluble fraction (Hanley 1980), nitrogen, mineral nutrients, and energy sources are closely related dietary constituents. Diets that are high in digestible energy also tend to be high in nitrogen and essential minerals as well. The microflora in the rumen synthesizes B-complex vitamins, and vitamin deficiencies appear to be rare (Short 1981).

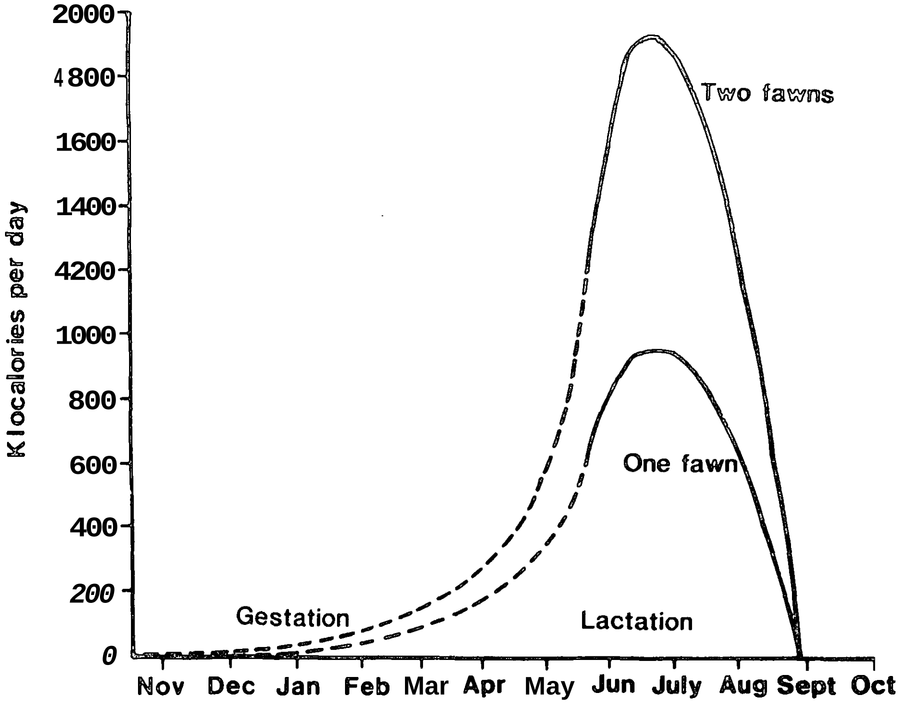

Figure 4.—Energy required for gestation and lactation by a doe with one or two fawns (Source: Moen 1973, Robbins and Moen 1975).

Plants also contain compounds that are deleterious to deer. Many such compounds have been considered secondary by-products of plant metabolism, but more recently their effects have been viewed as "anti-herbivore defense mechanisms" (Feeny 1976, Levin 1976, Rhoades and Cates 1976). Plant secondary compounds are basically of two kinds: (1) toxins and (2) digestibility-reducing substances. While most plants employ both kinds of compounds, one or the other usually predominates in certain types of tissue. Toxins tend to be very specific and dose-dependent, so their effects can be reduced or avoided by herbivores that consume a mixed-species diet. Digestibility-reducing compounds are more general and not dose-dependent, so their effects may be more difficult for herbivores to overcome. Digestibility-reducing compounds commonly interfere directly with nitrogen availability by forming indigestible complexes with proteins and enzymes (Feeny 1975, Mould and Robbins 1981), thus reducing the available nitrogen below the level indicated by the actual nitrogen content of the forage.

The content of secondary compounds varies with species and among individuals within species, and deer may select among them accordingly (Dimock and others 1976, Radwan 1972, Radwan and Crouch 1974). When deer are selective for this or other reasons, the amount of forage available is less than the current annual growth of the plants. Although maximizing energy intake may be a dietary goal, constraints are imposed by the deer's minimum requirements for nutrients and maximum tolerance of secondary compounds. Because chemical composition differs greatly among species, forage variety and a mixed diet are very important to deer (Carpenter and others 1979, Freeland and Janzen 1974, Milchunas and others 1978, Mould and Robbins 1981, Westoby 1974).

Diet composition.—A list of plant species known to be eaten by Sitka black-tailed deer can be obtained from the literature (table 2). Food selection has been reviewed recently by Crouch (1979), Taber and Hanley (1979), and Pierce (1981). Lists of species eaten, however, provide little information about diet selection and the relative importance of constituents. Of greater value is an understanding of the forage characteristics most valuable to deer (Hanley 1982a). The potential quality of forage is based on the relative content of cell solubles and cell-wall materials (table 3).

Although limited, data from southeastern Alaska (table 4) indicate that forages are similar chemically to those in western Washington (Hanley 1980) and Vancouver Island, British Columbia (Rochelle 1980). During the growing season, growing plant tissue (especially shrub leaves and forbs) contains the greatest proportion of cell solubles and nitrogen and is the most valuable deer forage. Plants growing in subalpine and alpine habitats are especially nutritious during summer (Klein 1965). During winter, evergreen shrubs and forbs (for example, bunchberry dogwood, five-leaved bramble, goldthread, foamflower, and pyrola) are the most valuable (Schoen and Wallmo 1979). Although deer eat deciduous shrubs and conifer foliage, herb-layer forages, if available, comprise the major portion of their diet (table 5). Where available, arboreal lichens (for example, beard lichen and alectoria) are readily eaten. They are a valuable energy source and may increase the digestibility of other forages (Rochelle 1980).

Table 2—Plant species reported to have been eaten by Sitka black-tailed deer

Species	Source
Forbs:	
Aruncus sylvester	Pierce 1981
Caltha biflora	Klein 1963
Caltha palustris	Pierce 1981
Coptis aspleniifolia	Merriam 1970, Reynolds 1979
Coptis trifolia	Merriam 1970
Epilobium angustifolium	Merriam 1965, 1968; Pierce 1981
Fauria crista-galli	Klein 1963, Merriam 1971a, Pierce 1981
Heracleum lanatum	Merriam 1964
Listera spp.	Klein 1965
Lysichiton americanum	Klein 1963, Merriam 1971a, Pierce 1981
Maianthemum dilatatum	Merriam 1965, 1967; Reynolds 1979
Potentilla spp.	Pierce 1981
Streptopus spp.	Merriam 1965
Tiarella trifoliata	Merriam 1965, 1967; Reynolds 1979
Vicia gigantea	Pierce 1981
Viratrum viride	Merriam 1965
Ferns:	
Athyrium filix-femina	Smith 1979
Blechnum spicant	Pierce 1981
Dryopteris spp.	Merriam 1965, 1967
Polystichum munitum	Klein 1963
Pteridium aquilinum	Pierce 1981
Thelypteris limbosperma	Pierce 1981
Graminoids:	
Calamagrostis spp.	Merriam 1964
Carex spp.	Klein 1963
Deschampsia spp.	Merriam 1964
Elymus arenarius	Olson 1952
Unspecified species	Merriam 1968; Pierce 1981
Half-shrubs:	
Cornus canadensis	Merriam 1965, 1967, 1970. and 1971a; Pierce 1981; Reynolds' 1979
Empetrum nigrum	Pierce 1981
Empetrum spp.	Merriam 1968
Loiseleuria procumbens	Pierce 1981
Oxycoccus microcarpus	Smith 1979
Rubus pedatus	Merriam 1965, 1967, 1970; Reynolds 1979
Vaccinium uliginosum	Klein 1963
Shrubs:	
Arctostaphylos uva-ursi	Merriam 1968
Betula spp.	Smith 1979
Cladothamnus pyrolaeflorus	Pierce 1981
Gaultheria shallon	Pierce 1981
Menziesia ferruginea	Klein 1957b, Pierce 1981
Oplopanax horridum	Klein 1963
Ribes spp.	Pierce 1981
Rosa nutkana	Merriam 1964
Rubus spectabilis	Merriam 1964
Rubus spp.	Pierce 1981
Salix spp.	Merriam 1968
Sambucus racemosa	Klein 1963, Merriam 1964, Pierce 1981
Vaccinium spp.	Klein 1957a, 1957b, 1963; Merriam 1965, 1967, 1968, 1970, 1971a, 1971b; Merriam and Batchelor 1963; Olson 1952; Olson and Klein 1959; Pierce 1981
Viburnum edule	Smith 1979, Pierce 1981
Trees:	
Alnus spp.	Merriam 1968
Chamaecyparis nootkatensis	Pierce 1981
Picea sitchensis	Klein 1963, Merriam 1968
Pinus contorta	Pierce 1981
Thuja plicata	Pierce 1981
Tsuga heterophylla	Klein 1963, Merriam 1965, Olson 1952, Pierce 1981
Tsuga mertensiana	Klein 1957b
Lichens:	
Unspecified species	Pierce 1981, Smith 1979
Mosses and Liverworts	
Unspecified species	Pierce 1981
Algae:	
Fucus spp.	Olson 1952

Table 3—Cell wall composition and estimated digestibility of some major classes of deer forage[1]

Food	Cell solubles	Cell wall	Holocellulose	Lignin	Estimated digestibility	
			Percent dry weight			
					A [2]	*B* [3]
Grasses:						
Immature	63	37	33	4	87	94
Mature	15	85	70	15	56	20
Forbs:						
Immature	56	44	33	11	71	69
Mature	25	75	57	18	53	27
Woody twigs:						
Immature	64	36	24	12	73	75
Mature	38	62	39	23	52	40
Leaves:						
Green	69	31	18	13	73	71
Fallen	51	49	23	26	50	45
Fleshy fruits	59	41	21	20	64	69
Mushrooms	61	39	37	2	93	95
Lichens (*Alectoria sarmentosa*)						[4] 73

[1] Source: Short 1981.

[2] *A* is estimated true dry-matter digestibility based on cell wall content and composition.

[3] *B* is estimated true dry-matter digestibility measured by the nylon-bag technique.

[4] Annual mean, from Rochelle (1980) for in vitro dry-matter disappearance.

Table 4—Chemical composition of 11 winter forage species collected in January[1]

Species	Cell solubles	Cellulose	Hemi-cellulose	Lignin/cutin	Ash	Nitrogen
			Percent			
Pyrola secunda	78.3	15.1	3.0	3.0	0.6	3.14
Tiarella trifoliata	76.3	18.3	2.4	2.6	.4	2.00
Rubus pedatus	67.3	17.3	11.0	3.8	.6	1.94
Cornus canadensis	66.8	18.1	6.8	7.8	.5	1.66
Coptis aspleniifolia	61.1	25.4	8.2	4.7	.6	1.62
Rubus spectabilis	36.0	27.5	16.8	18.7	1.0	1.79
Tsuga heterophylla	54.8	24.3	5.5	14.8	.6	1.50
Vaccinium spp.	37.9	29.8	13.1	17.4	1.8	1.46
Menziesia ferruginea	38.5	25.5	15.4	19.0	1.6	1.39
Usnea spp.	84.0	2.7	11.8	1.3	.2	.56
Liverwort	49.2	20.6	23.4	3.0	3.8	1.89

[1] Calculated from data in Schoen and Wallmo (1979, p. 80).

Table 5—Plant species composition of rumen contents from 14 Sitka black-tailed deer collected during virtually snow-free conditions at sea level on Admiralty and eastern Chichagof Islands, 1981[1]

Plant species	Rumen content (oven-dry weight) January (n=4)	February (n=9)	March (n=1)	Mean (n=14)	Range
	Percent				
Forbs and ferns:					
Coptis asplenifolia	12.9	4.8	18.6	8.1	0 -18.6
Dryopteris dilatata	0	5.4	.1	3.5	0 -37.9
Lysichiton americanum	6.0	1.7	16.2	4.0	0 -18.6
Tiarella trifoliata	.4	2.8	.4	1.9	0 -11.5
Half-shrubs:					
Cornus canadensis	37.5	35.5	16.1	34.7	13.6-54.1
Empetrum nigrum	.1	0	0	[2]	0 - .3
Phyllodoce aleutica	0	0	5.5	.4	0 - 5.5
Rubus pedatus	10.4	6.0	6.0	7.3	1.1-31.9
Vaccinium vitis-idaea	.1	[2]	1.6	.2	0 - 1.6
Vaccinium spp. [3]	.7	1.0	1.9	1.0	0 - 2.9
Shrubs and trees:					
Chamaecyparis nootkatensis	0	15.7	.6	10.1	0 -46.8
Ledum palustre	4.8	.9	11.3	2.8	0 -18.9
Picea sitchensis	0	[2]	0	[2]	0 - .1
Rubus spectabilis	7.5	0	0	2.1	0 -17.0
Tsuga heterophylla	1.0	9.8	3.5	6.8	.4 -25.8
Vaccinium spp. stems	3.2	3.1	4.6	3.2	0 - 9.9
Unidentified stems	3.8	6.8	10.6	6.2	
Lichens:					
Usnea spp.	1.4	.6	.3	.8	0 - 3.0
Other lichens	.2	3.3	.3	2.2	0 -14.1
Graminoids	[2]	.1	.3	.1	0 - 1.0
Alga:					
Fucus furcatus	6.9	1.1	2.2	2.8	0 -16.8
Mosses	.1	.2	.1	.2	0 - .9
Unknown	2.9	.7	0	1.3	

[1] Source: D. E. Spalinger 1981, unpublished report on file at Forestry Sciences Laboratory, Juneau.

[2] Less than 0.05 percent.

[3] Decumbent, evergreen variety.

Accumulation of snow affects availability of forage species differentially. The lower, evergreen herb layer containing the higher quality forage is covered before the lower quality conifers and tall, deciduous shrubs (Harestad 1979). The effect of snow on forage quality is, in general, disproportionately greater than its effect on forage quantity. In winter, when the herb-layer, evergreen forages are buried, energy deficits increase greatly, despite the abundance of deciduous browse and conifers (Kucera 1976, Markgren 1971, Perzanowski 1978).

Forest Vegetation and Patterns of Habitat Use

Secondary succession.—The old-growth, commercial forest is characterized by uneven-aged stands that are more than 250 years old (Alaback 1980, Franklin and others 1981) and dominated by western hemlock and/or Sitka spruce, with an understory composed primarily of ericaceous shrubs, ferns, and forbs. Dominant trees tend to be massive, and the understory is relatively productive (–800 kg/ha) and rich in numbers of species (Alaback 1980, 1982). The successional sequence following windthrow is difficult to characterize, because the degree and frequency of disturbance ranges from scattered trees being blown down or dying to entire stands being blown down at once (Alaback 1980,1982). Windthrow of large trees or small groups of trees appears to be the most frequent type of disturbance in old-growth forests (Brady and Hanley 1984).

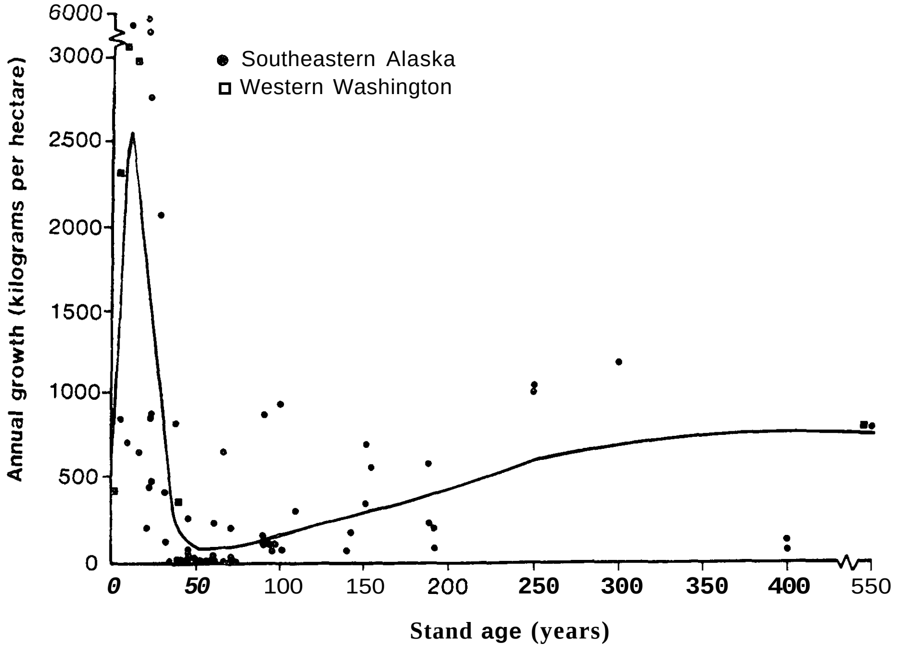

Figure 5. —Current annual growth of understory shrubs, forbs, ferns, and graminoids in relation to stand age for southeastern Alaska (Alaback 1980) and the Abies *amabilis* Zone of western Washington (Hanley 1980). Line has been fitted to means calculated at 10- to 20-year intervals.

Following clearcutting of relatively well-drained sites, shrubs dominate for the first 15 to 25 years and then young conifers take over (Alaback 1980, Harris 1974). Following closure of the canopy in young conifer stands, vascular understory species are virtually eliminated for about a century before they begin to reestablish themselves (Alaback 1982). Availability of the current annual growth of vascular understory species fluctuates greatly during this successional sequence, ranging from as high as 5 500 kilograms per hectare at about 20 years to zero at 50 years (fig. 5). This pattern is similar to that in the coastal Pacific Northwest (Hanley 1980, fig. 5), except that up to about 30 years levels of shrub biomass produced tend to be much greater in southeastern Alaska, while from 30 to 150 years levels of understory biomass and production tend to be much lower (compare Aiaback 1980, Hanley 1980, Long 1976, Long and Turner 1975, Turner and Long 1975). There is also a striking lack of dominant herbs following clearcutting in southeastern Alaska. For example, the current annual growth of herbaceous vegetation in clearcuts 8 to 13 years old in the Cascade Range of western Washington was 2 100 kilograms per hectare (Hanley 1980) compared to about 400 kilograms per hectare in southeastern Alaska (Alaback 1980); respective levels of current annual growth of shrubs were 1 100 versus 2 400 kilograms per hectare.

The possibilities of modifying secondary succession in southeastern Alaska by silvicultural treatment are being investigated, but the responses of understory species are poorly understood (Kessler 1982). Also of unknown'consequence is the pattern of secondary succession following logging of second-growth stands without vascular understories. Widely dispersing, adventitious species may become increasingly common in young clearcuts (Brady and Hanley 1984).

If carrying capacity for deer is directly proportional to the production of forage in a particular habitat, then carrying capacity should increase immediately following clearcutting of the old growth and decrease with canopy closure of the second growth (Brown 1961). Besides the quantity of forage produced, however, it is important to consider what forage is available, especially in winter. The frequency, depth, and duration of snowpacks are critical in the relationship between forage production and carrying capacity for deer. More snow accumulates in recent clearcuts than in forests, thereby reducing the availability of forage and increasing the energy costs of travel for deer (Fitzharris 1975; Gates 1968; Harestad 1979; Jones 1974, 1975; Schoen and Wallmo 1979; Weger 1977). Under snow conditions, the carrying capacity of old-growth forests is much greater than that of any earlier seral community (Harestad and others 1982). Arboreal lichens that are important sources of energy for deer during winter are available in significant quantities only in old-growth forests (Bunnell 1979, Bunnell and Eastman 1976, Rochelle 1980).

Wallmo and Schoen (1980), working on southern Admiralty Island and eastern Chichagof Island, examined deer use of old-growth and younger stands. Data based on fecal pellet groups revealed that during both summer and winter deer used old-growth forest more than recent clearcuts or closed-canopy second-growth forest (fig. 6). Virtually identical patterns have been observed during winter on Annette Island on the southern end of the Alexander Archipelago (Rose 1982). Farther south, on Vancouver Island, British Columbia, old-growth forest was preferred during winter (Bunnell 1979, Harestad 1979, Jones 1974 and 1975, Rochelle 1980), but recent clearcuts were used more heavily during summer (Harestad 1979). This was also true on summer range in western Washington (Hanley 1980).

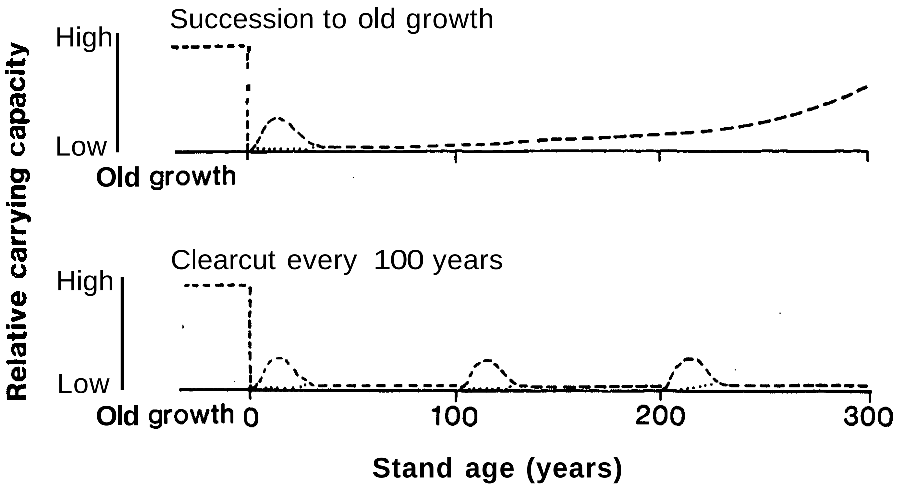

Figure 6.—Hypothesized changes in carrying capacity for deer of western hemlock-Sitka spruce forest in southeastern Alaska. In recent clearcuts, winter carrying capacity may be reduced to zero by snow (adapted from Wallmo and Schoen 1980, used with permission).

Table 6—Preliminary classification of 3 southeastern Alaska forest overstory types that comprise most of the commercial forest land[1]

Overstory type (Level IV)	Community type (Level V)
Sitka spruce--occupies wet sites, primarily alluvial flood plains	*Picea sitchensis/Oplopanax horridum-Rubus spectabilis/Cornus canadensis*
Sitka spruce-western hemlock--occurs on moist sites	*Picea sitchensis-Tsuga heterophylla/Lysichiton americanum/Sphagnum* spp. *Picea sitchensis-Tsuga heterophylla/Vaccinium ovalifolium-V. alaskensis-Menziesia ferruginea* *Picea sitchensis-Tsuga heterophylla/Moneses uniflora-Tiarella trifoliata/Mnium* spp.
Western hemlock-Sitka spruce-(western redcedar)--widespread throughout southeastern Alaska	*Tsuga heterophylla-Picea sitchensis-(Thuja plicata)/Vaccinium ovalifolium-V. alaskensis/Rhytidiadelphus loreus*. *Tsuga heterophylla-Picea sitchensis-(Thuja plicata)/Lysichiton americanum/Sphagnum recurvum*.

[1] Viereck and Dyrness, 1980.

The central assumption of all of these studies is that use of habitat is roughly proportional to habitat quality (capacity to produce and/or support deer). This assumption is well founded on theoretical grounds (Brown 1969; Doyle 1975; Fretwell 1972; Fretwell and Lucas 1970; Lack 1954; Levins 1962, 1968; Orians 1980; Templeton and Rothman 1974). On northern Vancouver Island, however, evidence is mounting that deer populations actually decline following logging (Hebert 1979) as would be predicted by models based on habitat use (Harestad 1979, Wallmo and Schoen 1980).

Variation within the forest.—Viereck and Dyrness (1980) listed 14 forest overstory types found in southeastern Alaska. Only 3 of the 14 comprise a substantial proportion of the commercial forest lands: (1) Sitka spruce, (2) Sitka spruce-western hemlock, and (3) western hemlock-Sitka spruce-(western redcedar). The latter two types intergrade almost imperceptibly with one another. Although Viereck and Dyrness tentatively subdivided these three types into six community types (table 6), much work lies ahead to identify patterns of species associations in forest understories in southeastern Alaska.

Schoen and others (1981) identified three major understory species associations within the commercial spruce-hemlock forests on eastern Chichagof and Admiralty Islands: (1) huckleberry/bunchberry dogwood-five-leaved bramble-goldthread, (2) devilsclub/skunk cabbage-violet-foamflower, and (3) single delight-conifer seedlings. When individual stands were plotted in relation to principal components, however, no distinct community types were evident, indicating that the species associations were best considered as gradients rather than community types per se.[2] The huckleberry/bunchberry dogwood-five-leaved bramble-goldthread association was most common on well-drained sites. The devilsclub/skunk cabbage-violet-foamflower association was most common on wet sites, with devilsclub dominating on shallow, rocky soils with flowing water and skunk cabbage dominating on poorly-drained, mucky soils with standing water. The single delight-conifer seedling association appeared to be related to dead and down debris where single delight and conifer seedlings became established above the underlying forest floor. This association, therefore, appeared to be independent of the other two associations. These analyses are tentative, however, and need further work.

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[2] Schoen, J. W.; Kirchhoff, Matthew D.; Hanley, Thomas A. Unpublished data on file at Forestry Sciences Laboratory, P.O. Box 909, Juneau, AK 99802.

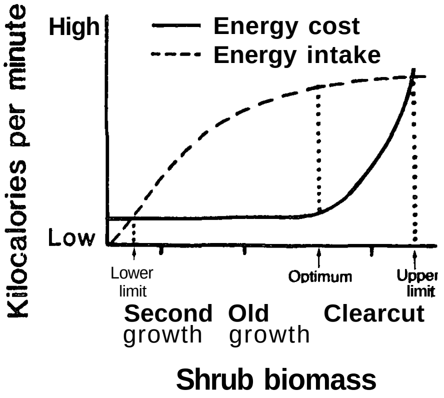

Figure 7.—A foraging benefit-cost model of habitat selection in southeastern Alaska old-growth commercial forest, recent clearcuts, and closed-canopy second-growth forest. Deer should prefer habitat where the difference between energy intake and energy cost is greatest. There is an optimal level (or range of levels) of shrub biomass as well as lower and upper limits where energy intake is not less than energy costs.

The forest overstory influences the understory through its effect on microclimate and availability of both above- and below-ground resources. Understory production tends to be negatively associated with overstory vigor and density, but the relationships between variables vary with stand structure (Alaback 1980). In Alaback's analysis of 62 stands, understory production was negatively correlated with overstory canopy coverage, foliar biomass, and stand volume in young (<90 years), even-aged, second-growth stands but was positively correlated with mean tree diameter, basal area, and stand volume in mature (>90 years), even-aged and uneven-aged, old-growth stands. The positive correlations in mature and old-growth stands were related to increased space between large trees, which was accompanied by an increase in mean tree diameter and volume as stands aged. Increased space accompanies breaking up of the canopy, as stands age beyond silvicultural maturity and understory biomass and productivity increase (Bormann and Likens 1979, Franklin and others 1981).

In southeastern Alaska forests, patterns of habitat use by deer have been studied most intensively during winter and early spring—seasons when deer depend most heavily on forests. Studies (Barrett 1979; Bloom 1978; Leopold and Barret 1972; Rose 1982; Schoen and others 1979, 1981) show that the habitats of greatest value to deer during periods of snow accumulation are old-growth, western hemlock-Sitka spruce forest of moderate to high volume (>≈20,000 board feet per acre), with an understory of huckleberry, bunchberry dogwood, and five-leaved bramble. This combination of structural and compositional characteristics apparently resulted in a high degree of snow interception and redistribution by the massive forest canopy, as well as high-quality, nutritious forage available in the understory.

During snow-free periods, however, the relative importance of habitats may shift. Herb-layer, evergreen plants (for example, bunchberry dogwood and five-leaved bramble) continue to be the forage of highest quality, but may be more available in more open-canopied, lower-volume forests (Schoen and others 1982).

Wet sites with an understory dominated by devilsclub or skunk cabbage received less use during winter than well-drained sites with understories dominated by huckleberry (Schoen and others 1981). During early spring, however, skunk cabbage is one of the first species to produce new growth above ground, and deer use it heavily (Klein 1965). Forest patches where skunk cabbage is abundant receive high use by deer during this relatively brief but important time.

Patterns of forest use by deer, therefore, shift through the winter and spring with changes in snow conditions and plant phenology. Although moderate- to high-volume, old-growth, western hemlock-Sitka spruce forests with an understory of huckleberry, bunchberry dogwood, and five-leaved bramble may be the most important kind of habitat for deer during deep snow accumulations, other kinds of forested habitat may be of greater value during snow-free periods. Variety of habitat on the winter range is important.

A benefit-cost model of habitat quality.—Why might old-growth forest be preferred to recent clearcuts that are snow-free, even during summer? This pattern of habitat use appears, superficially, to be contrary to the behavior of black-tailed deer in more southern latitudes. Wallmo and Schoen (1980) suggested that logging slash may be the primary factor that restricts deer use of recent clearcuts during snow-free periods. Another hypothesis is that deer use clearcuts less because forage quality is lower. This is based on data presented by Billings and Wheeler (1979), Van Horne (1982), and Rose (1982) that indicates nitrogen content of understory plants is greater in old-growth understory than in clearcuts. A third hypothesis is that in southeastern Alaska deciduous shrubs quickly form such dense stands that any benefits from increased forage availability in clearcuts are more than offset by increased energy costs of travel.

All three of these hypotheses could be correct and interactive, as illustrated in a simple, generalized model of habitat selection (fig. 7). As the biomass of herb- and shrub-layer vegetation increases, intake of metabolizable energy increases rapidly at first and then levels off at a saturation level. It is also assumed that energy costs of locomotion are low and relatively stable when levels of shrub biomass are low and medium but increase exponentially when levels of shrub biomass are high. Habitat quality is measured by the difference between intake and cost, with optimal habitat being the level at which intake minus cost is maximum. Costs of foraging exceed benefits when levels of biomass are either very low or very high. At the points where the two functions intersect, costs are equal to benefits.

Even-aged second-growth, uneven-aged old-growth, and recently clearcut habitats in southeastern Alaska should have low, medium, and high levels of shrub biomass as shown on the gradient in figure 7. If this is the case—as it appears to be—snow-free clearcuts in western Washington and Oregon, with lower peak levels of shrub biomass than those in southeastern Alaska, should be of greater value to deer.

Additional support of this model comes from the convex parabolic curves that Willms (1971:85-96) observed for the relationship between deer use and shrub canopy coverage on Vancouver Island. Willms noted that densities of deer pellets in clearcuts were positively correlated with low and medium levels of shrub cover but were negatively correlated with high levels of shrub cover. This relationship would be predicted from figure 7.

The benefits and costs depend on more than availability of forage and amount of shrub biomass. Forage quality is important (Moen 1973, Wallmo and others 1977), as well as relationships involving thermal energy exchange (Beall 1974, Moen 1973), amount of logging slash (Lyon 1976, Lyon and Jensen 1980), and snow depth (Drolet 1976, Gilbert and others 1970). These factors can be incorporated into the model by altering the benefit and cost curves.

Differences in forage quality affect intake. As forage quality increases, the net intake of metabolizable energy (that is, foraging efficiency) increases (fig. 8a). This results from greater nutrient value per unit of forage and a greater passage rate of ingested forage. With the latter, deer have opportunities for more bites per unit of time and/or more time for selecting bites (Hanley 1982b). As forage quality increases, the difference between energy intake and energy cost increases. The reverse is true where forage quality decreases.

Difference in the thermal environment may also affect foraging costs. As thermal energy losses from deer increase, the energy expended by deer to maintain homeothermy increases (fig. 8b). Costs of thermal energy exchange are in addition to foraging costs (Moen 1973) and raise or lower the cost curve with little or no effect on its shape. As thermal energy costs increase, the difference between energy intake and energy cost decreases.

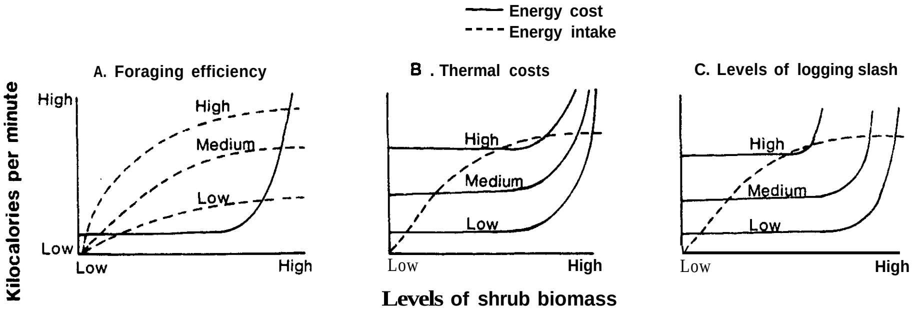

Figure 8.—Factors that interact to affect the benefit-cost relationships for deer.

Depth and amount of logging slash also affect foraging costs. If the effects of logging slash and shrub biomass are interactive (that is, each exaggerates the effect of the other), the result is raising the cost curve and sharpening its inflection with increases in logging slash (fig. 8c). As the amount of logging slash increases, the difference between energy intake and cost decreases. While changes in forage quality, thermal environment, or amount of logging slash affect the range of habitats that are suitable for deer, only changes that interact with shrub biomass (in this case, logging slash) affect the level of shrub biomass considered to be optimal.

The effects of snow are more complicated. As snow depth increases, forage availability and quality decrease and foraging costs increase. In general, energy requirements increase exponentially with snow depth, while food availability decreases (fig. 9). If the snow is capable of supporting a deer's weight, then it effectively reduces the level of shrub biomass available and the amount of slash. Snow reduces forage quality by burying the herb-layer plants but may or may not add to the energy costs of travel, depending on the depth to which the deer sinks. The overall effect of snow is to restrict the range of suitable habitats and to lower the quality of all habitats.

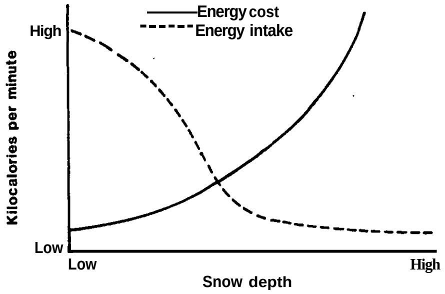

Figure 9.—A benefit-cost model illustrating the effect of snow depth on the energy intake of deer and energy costs of foraging (adapted from Harestad and others 1982, used with permission).

The problem faced by the deer is choosing the habitat patch and diet where the foraging benefit is greatest. Choice of habitat determines foraging costs; the amount of forage available and choice of diet determine energy intake.

Home Range

To a large extent, the movements of an individual deer are confined to a limited area known as home range. Deer, especially females, appear to learn their home ranges from association with their mothers during their first year or two (Dasmann and Taber 1956, Nelson and Mech 1981). Fidelity to their traditional home ranges can be so great that deer will starve to death rather than travel a few kilometers to abundant forage (Dasmann and Taber 1956). The summer home ranges of migratory deer are usually larger than their winter home ranges, and bucks tend to have larger home ranges than does. Bucks are also more mobile and more likely to establish new home ranges than does (Dasmann and Taber 1956, Miller 1970, Nelson and Mech 1981, Robinette 1966). Home range determines what habitats are available to individuals, and, to a large degree, tradition determines the distribution of deer over the landscape (Nelson 1979). Since quality of habitat is not uniform, some deer fare better than others (Taber and Dasmann 1957).

Home ranges of deer in southeastern Alaska (Schoen and others 1981) are comparable in size to those reported for Columbian black-tailed deer in the Pacific Northwest (Hanley 1980, Harestad 1979, Miller 1970). Variation between individual deer probably reflects differences in early experience as well as the habitat composition of their home ranges (Schoen and others 1981). About two thirds (11 of 17) of the Sitka black-tailed deer captured on winter range and monitored the year around by telemetry by Schoen and others (1982) made distinct migrations between winter and summer ranges; the other six were year-round residents of their winter ranges. All 13 deer for which 2 or more years of data were available utilized similar summer and winter home ranges between years, suggesting strong fidelity to home ranges (Schoen and others 1982). “Migratory” deer generally summer at relatively high elevations, while “resident” deer remain in low-elevation habitats the year around. This phenomenon is common with Columbian black-tailed deer in the coastal Pacific Northwest as well (Harestad 1979, Taber and Hanley 1979). S

Seasonal movements.-In early spring, most deer in southeastern Alaska are still on winter range, which is usually below 300 m (Klein 1965, Schoen and others 1981). Upper elevations vary from 100 m during years of heavy snow accumulation and/or on northerly exposures, to 600 m during light snow and/or on southerly exposures. As the snowline recedes, deer move up and make greater use of areas with new, green vegetation. By late spring, high quality forage is abundant, and migratory deer move near their summer ranges. Spring home ranges of 13 telemetered deer reported by Schoen and others (1981) ranged from 30 to 12 369 ha and averaged 1 521 ha. Distances (straight-line) between summer and winter ranges for telemetered migratory deer have been observed between 1.6 and 72.5 km (Schoen and others 1981). Most deer probably move less than 10 km between winter and summer home ranges. In general, spring is a transition period between summer and winter ranges for migratory deer. For resident deer, some of which spend the whole year—and perhaps their entire lives—within 200 ha, only localized shifts occur. Parturition occurs in late May and early June, usually in lower elevation habitat.

During summer, migratory deer on the mainland and larger islands have access to abundant, high quality forage in alpine and subalpine habitats (Klein 1965) and prefer these habitats (Schoen and others 1981). The summer home ranges of the 13 telemetered deer reported by Schoen and others (1981) ranged from 40 to 563 ha, and averaged 233 ha. They were distributed from sea level (resident deer) to above 1 000 m (migratory deer).

The fall home ranges of 12 telemetered deer reported by Schoen and others (1981) averaged 505 ha and ranged from 64 to 1 307 ha. Migratory deer continue to utilize alpine and subalpine habitats through early fall. After the first heavy frosts, when much of the herbaceous forage is killed, deer move down to the upper forest. They may remain at higher elevations throughout fall unless snow begins to accumulate. Some deer move up and down with the changing snowline (Schoen and others 1979, 1981). Some move to lower elevations following the first snow and stay there; others remain in areas where snow accumulations exceed 30 cm. During the rut from late October to early December, migratory and resident deer probably are not segregated.

Winter through early spring is the period of greatest year-to-year variation in deer distribution. It also is the period when forage is most limited and the time of highest mortality. Winter home ranges of 15 of the telemetered deer reported by Schoen and others (1981) ranged from 42 to 302 ha and averaged 122 ha. In some years, elevations below 300 m are nearly free of snow throughout the winter. In other years, snow may accumulate below 150 m for **4** to 5 months, with extensive snow at sea level. Early winter snow seldom remains long at lower elevations because of the strong maritime influence. As rain melts the snow, many migratory deer that moved to lower elevations after the first snow move, again, into the higher forest, often as high as 600 m or higher (Schoen and others 1981, 1982). Throughout the winter resident deer also move up and down within their home ranges depending on changing snow levels. It appears that many deer winter as high as snow conditions allow (Barrett 1979, Merriam 1968, Olson 1952, Schoen and others 1981). The mean elevation for 12 telemetered deer during two mild-to-average winters on Admiralty Island was 111 m, with individual variation from 30 to 237 m (Schoen and others 1981). Individual animals varied greatly in mean distance from the beach. When snow is deep at sea level, the beach and beach-fringe forest become the last refuge for many deer. In less severe conditions, the best winter habitat may be many kilometers from the beach.

Deer affect vegetation through selective consumption of plants and plant parts, and by trampling. As a result, palatable woody stems and succulent forbs with growing tissue located above ground tend to decrease, while graminoids and forbs with growing tissue at or below the ground surface may increase (Hanley and Taber 1980). If deer are abundant, they may create an open-appearing landscape (Hanley and Taber 1980).

Management Implications

Deer severely altered the vegetation on Coronation Island in southeastern Alaska (Klein 1965). Deer use resulted in "hedged" forms of ovalleaf huckleberry, red huckleberry, red elderberry, and even western hemlock and Sitka spruce. Klein believed that excessive use by deer had eliminated important winter and summer forage species on the island. Similarly, high populations of introduced Sitka black-tailed deer on the Queen Charlotte Islands in British Columbia, have affected the vegetation so heavily that foresters are concerned about future regeneration of western redcedar, Alaska yellow cedar, western hemlock, and even Sitka spruce.[3] Damage to young Douglas-fir has been a problem for foresters in the Pacific Northwest for many years (Cowan 1945, Crouch 1981). Moderate levels of browsing, however, may reduce competition by shrubs and benefit young conifers (Crouch 1974, Hanley and Taber 1980).

As sources of high quality forage decrease, deer consume lower quality forage, resulting in decreased quality of diet (Carpenter and others 1979, Klein 1965, Taber and Dasmann 1957). The effects of decreased diet quality on Sitka black-tailed deer were demonstrated in Klein's (1962, 1964, 1965) comparisons of deer populations and their habitat on Woronkofski and Coronation Islands in southeastern Alaska. For a variety of reasons, including mild winter weather and the absence of wolves on Coronation Island, deer populations there were believed to exceed the normal carrying capacity of their habitat, with a resulting decrease in high quality forage. Deer on Woronkofski Island, in contrast, had access to a greater proportion of alpine and subalpine habitat in summer, but were subject to more severe winter weather and wolf predation. They exceeded the carrying capacity of their habitat much less often than the deer on Coronation Island. Deer on Coronation Island had lower body weights and growth rates, a lower ratio of fawns to adult females, an older average age, a less even sex ratio, and higher natural mortality in young animals than deer on Woronkofski Island. These attributes are characteristic of lower quality diet.

The habitat relationships of Sitka black-tailed deer provide only a general perspective for evaluating local conditions and circumstances and for developing management prescriptions. Specific situations in each area must be considered. In southeastern Alaska the variation in natural vegetation and climate are particularly important. The amount and quality of vegetation varies within both old-growth and second-growth forests. Climate varies both spatially and temporally. Snow influences forage availability and is critically important in managing habitat for both deer and timber. The frequency, depth, and persistence of snow varies greatly throughout the range of Sitka black-tailed deer and often over very short distances. Topography and prevailing climate are major factors which must be considered in developing local management prescriptions.

Wolf predation can be a significant factor in controlling deer populations in southeastern Alaska (Klein 1981). Although little is known about deer-wolf relationships in this region, where wolves are present, deer populations probably are slow to recover from die-offs during the occasional severe winters. Theoretically, if the fecundity of a deer population declines below a threshold level, a rapid decline in deer density is likely to result, with predation as the proximate cause (Van Ballenberghe and Hanley 1984). Management practices that lower the carrying capacity of the habitat can initiate population declines. Management to maintain habitat and prevent declines in deer populations seems more logical than trying to reverse deer declines by controlling wolves (Van Ballenberghe and Hanley 1984).

Although management prescriptions must be based on local circumstances, general principles could be applied universally: Understanding the functional relationships between deer and their habitat will help. Physiological requirements of deer under various environmental conditions can help define required and optimal habitats. Optimum habitat, however, cannot be defined in terms of specific structural or compositional features throughout the range of Sitka black-tailed deer. Optimal elevation, stand volume, or understory species composition, for example, vary with other environmental circumstances and are not fixed. Beyond understanding the functional relationships, the following guidelines may help focus attention on specific features of habitat.

Critical Winter Range

The concept of "critical winter range" means habitat that is of great importance for deer survival and is in relatively short supply during severe winter weather (in southeastern Alaska, periods of deep snow accumulation). Critical winter range is the optimal habitat during climatic conditions that are most responsible for winter mortality of deer. It is not optimal habitat under all winter conditions and, alone, it may not even be adequate to support deer throughout an entire winter. Other habitats are important for relieving browsing pressure on critical winter range during periods when snow is not deep.

From a deer perspective, there probably are three thresholds of snow depth. The first is the depth at which evergreen forbs and herb-layer shrubs become buried—approximately 10 cm. The second is when deer sink in the snow beyond front knee height (approximately 25 to 30 cm) and energy costs for locomotion increase greatly[4] (fig. 2). The third threshold is the point at which tall shrubs become buried. When snow is beyond that depth, deer diet consists almost entirely of low quality conifer foliage, and the energy costs for locomotion are extremely high. Crusting of the snowpack reduces sinking depth greatly, but forage remains buried. For management purposes, therefore, snow deeper than 25 to 30 cm probably should be considered "deep snow."

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[3] Pojar, Jim; Lewis, Terence; Roemer, H.; Wilford, D. J. Relationships between introduced black-tailed deer and the plant life of the Queen Charlotte Islands. British Columbia: B. C. Ministry of Forests. Unpublished report on file at Research Branch, B. C. Ministry of Forests, Smithers, B.C., Canada. VOJ 2NQ 1980. 63 p.

[4] Parker, K. L. and Robbins, C. T. (Dept. Zoology, Wash. State Univ.) Personal communication on file at Forestry Sciences Laboratory, P.O. Box 909, Juneau, AK 99802.

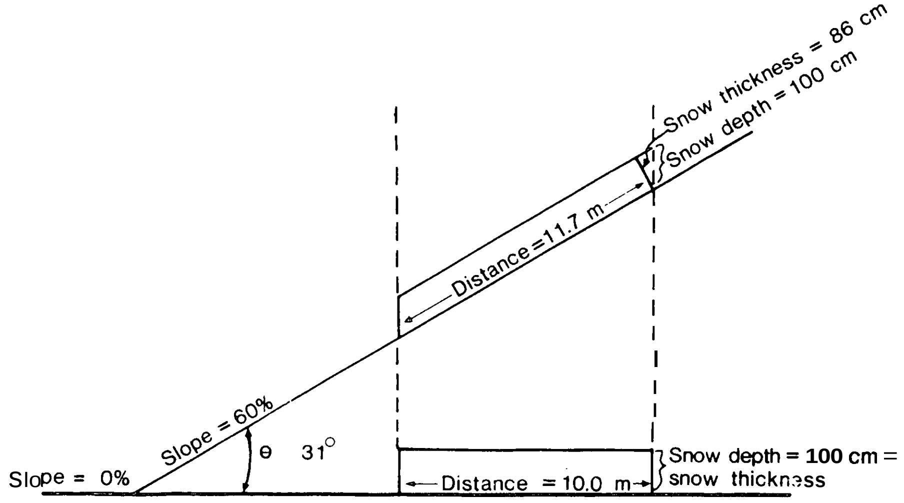

Figure 10.—Snow thickness is less on steep slopes than on moderate slopes or level areas because snow is spread over more ground surface. A slope of 60 percent (31") has a ground surface area 1.17 times that of a level area; hence, snow thickness is 86 percent that of the level area. Snow depth, however, is the same as on the level area.

Habitat features most useful in identifying critical winter range are climate, topography, and vegetation. Prevailing winter climate varies from frequent, heavy snowfall in the northeastern part of the Alexander Archipelago to relative absence of snow in the lower elevations of the Queen Charlotte Islands. The elevation of critical winter range may vary substantially. Beach-fringe forest is the last refuge under severe conditions, but better habitat away from the beach or higher in elevation should not be discounted as critical winter range simply because of its location.

The degree of slope influences snow depth by its effect on the ratio of surface area to horizontal area. Assuming that snow generally falls vertically, increasing slope steepness distributes a given amount of snow over an increasingly large area, resulting in more snow being exposed to air and radiant energy (fig. 10). Other conditions being equal, the rate of snow ablation (melting and vaporization) will be proportional to surface area, and snow accumulation will be negatively related to slope angle. Of course, slope aspect, shading, and other factors (wind speed, temperature, and vapor pressure deficit) are also important.

Southerly aspects are exposed to much more potential solar radiation than northerly aspects, and radiation increases with steepness of slope on southerly aspects and decreases on northerly aspects (fig. 11). Snow ablation varies accordingly. Steep southerly slopes are probably usable longer in fall, winter, and spring than shallow southerly slopes or any northerly slopes. Considering the low sun angle at northerly latitudes during winter and the steep topography of southeastern Alaska, shading of the slope by adjacent mountains may be another factor to consider (fig. 12). Unshaded, south-facing beaches and slopes may provide more suitable habitat than shaded ones.

Two features of forest vegetation that are of greatest importance for critical winter range are: (1) a productive understory of high-quality forage, and (2) an overstory that intercepts and/or redistributes sufficient snow for understory forage to remain available to deer. On eastern Chichagof and Admiralty Islands, these conditons apparently are met most satisfactorily by low- to mid-elevation (< 300 m), old-growth, hemlock-spruce stands of moderate to high volume (30,000 to 50,000 board feet per acre), with a canopy cover of 60 to 80 percent and an understory dominated by huckleberry, bunchberry dogwood, and five-leaved bramble (Schoen and others 1981, 1982). Even at moderate snow depths (10 to 25 cm), these stands seem to provide bare spots of ground immediately beneath large trees where the highly nutritious evergreen forbs and herb-layer shrubs remain available to deer. At greater snow depths (> 30 cm), the availability of huckleberry apparently is most important. Lichen litterfall also may contribute greatly to the quality of critical winter range (Rochelle 1980).

Habitat Protection

Variety of habitat on winter range is important for deer. Open-canopied stands with abundant understory probably are most valuable during snow-free periods. Partially closed stands are more valuable during periods of snow accumulation. Much of the forest land in southeastern Alaska is of low timber volume and/or on steep slopes and currently is classified noncommercial forest. This land could provide suitable habitat during snow-free periods in perpetuity. The moderate- to high-volume, old-growth, commercial forest is a smaller part of the total area and is the major area of concern in managing for both timber and deer habitat. In areas that have winters of frequent, high snowfall and have relatively limited critical winter range for deer, the amount of old-growth, critical winter range is likely to directly determine the carrying capacity for deer.

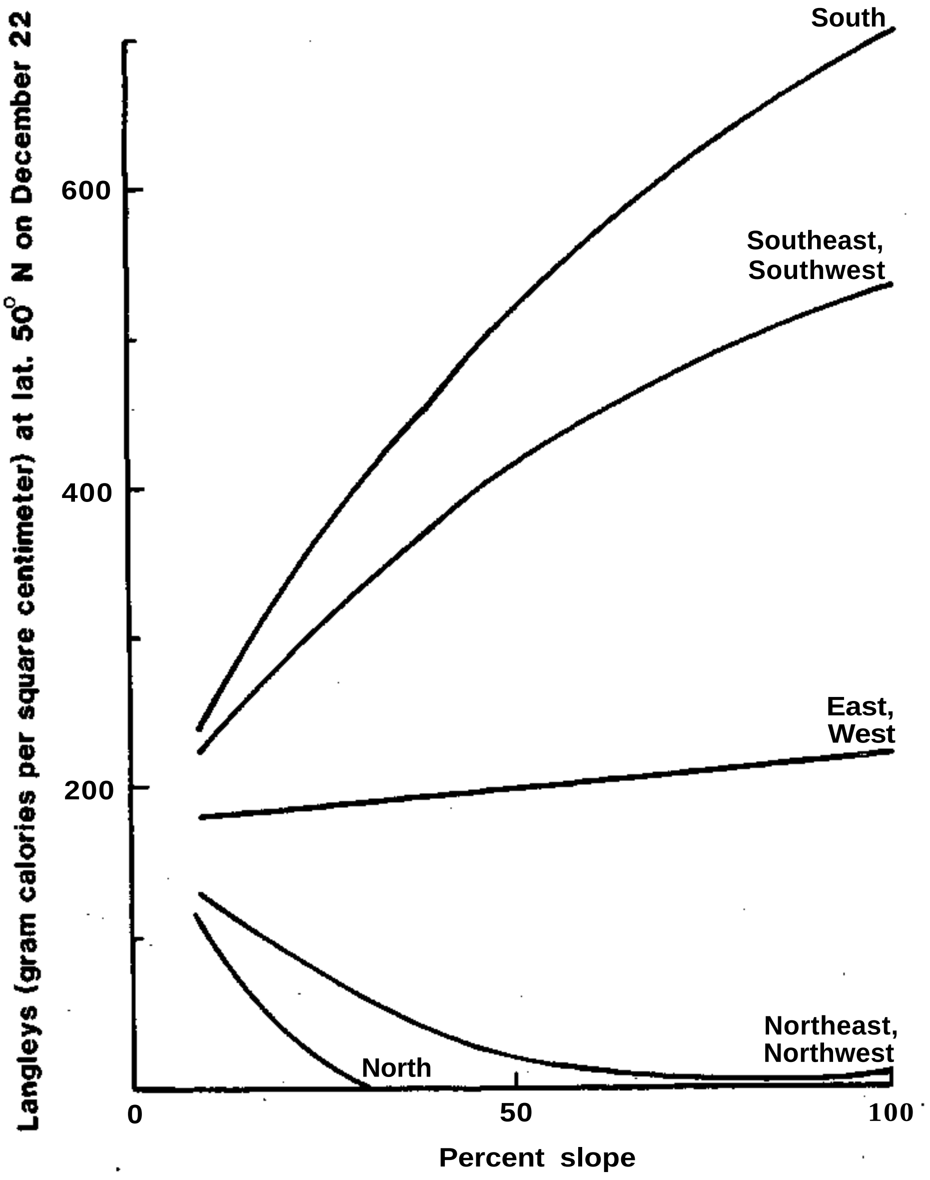

Figure 11 .—Effect of slope and £
potential solar irradiation.

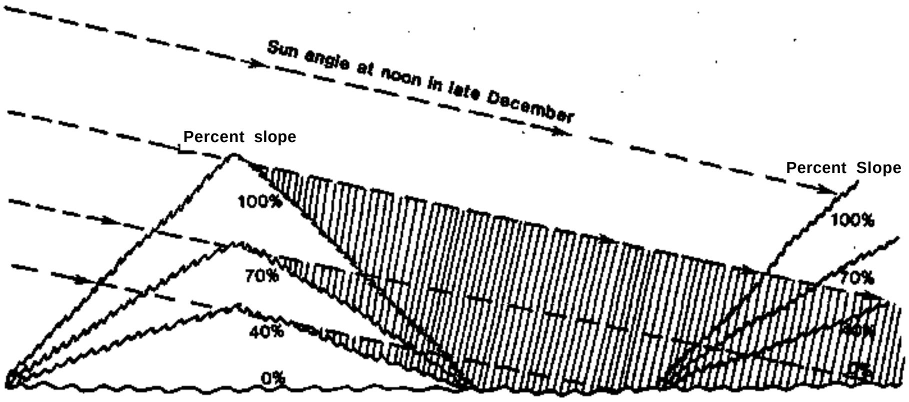

Figure 12.—Effect of slope, aspect, c
shading on solar irradiation of forest
Logging is normally restricted to slop
percent or less.

Retaining scattered blocks of old-growth forest within young, second-growth forest creates two potential problems. First, scattered patches of critical winter range potentially serve to concentrate deer, with resulting overuse of forage and decreased carrying capacity. Second, windthrow is common along the edges of clearcuts and may decrease the area of protected deer habitat. Both problems could be minimized by retaining patches of critical winter range that occur naturally within blocks of low-volume, noncommercial, or inoperable forest. Such protection would provide a variety of winter habitat within the home range of many deer and natural, wind-firm boundaries of high-volume areas. Deer with home ranges outside protected critical winter range would not know of its existence, thus minimizing problems of concentrated use.

Beach-fringe forest, the last refuge for deer moving downslope during periods of deep snow accumulation, is very important habitat that needs protection because it provides temporary but critical refuge. It cannot, however, sustain large numbers of deer for prolonged periods.

The importance of retaining areas of old-growth forest varies with the habitat composition of each management unit and the desired population levels of deer. Other factors are important also. Where the prevailing climate is mild and deep snow accumulations are rare and short in duration, a mosaic of young clearcuts within even-aged second growth probably can provide suitable winter range, as in coastal Oregon and Washington. This strategy might be appropriate management for the Queen Charlotte Islands, for example. There are no wolves on the Queen Charlottes, and deer populations would be expected to increase rapidly after an occasional, severe-winter die-off. Where wolves are present, however, the potential for recovery could be different and the long-term effects of occasional severe winters magnified.

Habitat Enhancement

Three silvicultural approaches can potentially improve deer habitat: (1) increasing forage quality, (2) increasing forage abundance and availability, and (3) improving accessibility. For recent clearcuts, the first and third are the most important; for closed-canopy, second-growth forest all three are important, but especially the first two.

Cleaning up logging slash and enforcing standards for timber utilization can reduce slash and improve deer accessibility in recent clearcuts that are free of snow. Broadcast burning in recent clearcuts also reduces slash and, sometimes, shrub biomass. Burning probably affects species composition, reducing shrubs and favoring herbs, a change that can affect quality and/or availability of deer forage. Losses of nitrogen through volatilization and leaching, however, may be an important negative consequence. Burning temporarily sets back conifer regeneration and prolongs the useful life of clearcuts for deer in snow-free seasons or areas. Precommercial thinning also may prolong the usefulness of recent clearcuts for deer if high levels of shrub biomass and/or slash do not decrease accessibility.

Precommercial and commercial thinning might improve deer habitat if they maintain and increase understory productivity and forage quality and intercept and redistribute snowfall so understory forage remains available. In either precommercial or commercial thinning, slash must be disposed of in ways that do not impede deer access.

The size and distribution of clearcuts in space and time are also important. Optimal sizes and placement are related to sizes of deer home ranges (Taber and Hanley 1979). The strong fidelity of deer to home ranges means they are unaware of habitat conditions outside their home range. Many small, scattered, irregularly-shaped clearcuts, therefore, are preferable to fewer, large, block-shaped clearcuts. Small clearcuts would result in a high ratio of forest edge to clearcut area, however, which could be a problem in areas prone to windthrow. The value of forest edge per se for deer is not well understood (Hanley 1983) and may be of no value in southeastern Alaska (Kirchhoff and others 1983).

It is important to spread the cutting over the entire elevational gradient. Clearcutting that begins at the lower elevations and moves upward results in a seral-stage gradient that is superimposed directly on the elevational gradient and severely limits deer options for finding quality habitat during winter.

Research Needs

Forest and wildlife managers need a means of quantitatively evaluating habitat quality for deer. Relationships among forest understory, overstory, and site need to be understood to predict understory species composition and productivity. Similarly, the chemical composition and nutritional value of forages need to be determined. Relationships among forest overstory, snow interception, and the availability of understory are very important. The metabolic requirements of deer and their relation to diet selection and habitat selection also are major factors. The theoretical framework for integrating these relationships into a quantitative model has been outlined in the preceding review and elsewhere[5] (Harestad and others 1982). A model based on functional relationships and driven by local climate and site factors would provide an objective means of evaluating habitat quality throughout the range of Sitka black-tailed deer.

In the short term, however, the most glaring lack of information concerns the size and productivity of deer populations. Although habitat preferences of deer have been demonstrated, population dynamics have not been studied. There are no data concerning the effects of logging on population sizes, densities, or other demographic parameters of Sitka black-tailed deer. A major reason for the lack of such information is that in habitats of dense forest, steep topography, and highly variable winter climate, it is extremely difficult to census deer populations. Nevertheless, adequate technology is a necessity for monitoring changes in deer populations and for testing the predictions of theory.

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As logging of old-growth forest continues, an increasing proportion of deer habitat, especially winter range, will consist of even-aged, second-growth forests. Unmanaged, these stands provide very poor deer habitat. Research is needed on silvicultural prescriptions to improve the habitat quality of second-growth stands. Techniques for applying the prescriptions and their effects also need to be evaluated.

Current research is focusing on these needs, specifically: (1) overstory-understory relationships within old-growth and second-growth forests; (2) overstory-snow relationships; (3) forage availability and nutritional quality; (4) diet composition and quality and energy intake; (5) energy expenditure; and (6) habitat selection. Research into population dynamics and monitoring techniques is also needed.

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Metric-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) = 4 186 joules
= 3.97 Btu
Celsius (C) = 5/9 (Fahrenheit − 32)

Scientific Names of Animal and Plant Species

Common name	Scientific name
Animals:	
Mule deer and black-tailed deer	*Odocoileus hemionus*
Sitka black-tailed deer	*Odocoileus hemionus sitkensis*
Columbian black-tailed deer	*Odocoileus hemionus columbianus*
Gray wolf	*Canis lupus*
Plants:	
Alaska yellow cedar	*Chamaecyparis nootkatensis* (D. Don) Spach
Alectoria	*Alectoria* spp.
Beard lichen	*Usnea* spp.
Bunchberry dogwood	*Cornus canadensis* L.
Devilsclub	*Oplopanax horridum* (Sm.) Miq.
Douglas-fir	*Pseudotsuga menziesii* (Mirb.) Franco
Fireweed	*Epilobium angustifolium*
Five-leaved bramble	*Rubus pedatus* Sm.
Foamflower	*Tiarella trifoliata*
Goldthread	*Coptis aspleniifolia*
Huckleberry	*Vaccinium* spp.
Ovalleaf huckleberry	*Vaccinium ovalifolium* Sm.
Pyrola	*Pyrola secunda*
Red huckleberry	*Vaccinium parvifolium* Sm.
Single delight	*Monesis uniflora*
Sitka spruce	*Picea sitchensis* (Bong.) Carr.
Skunk cabbage	*Lysichiton americanum*
Violet	*Viola* spp.
Western hemlock	*Tsuga heterophylla* (Raf.) Sarg.
Western redcedar	*Thuja plicata* Donn

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Old-growth, western hemlock-Sitka spruce forest in southeastern Alaska is an important element of the habitat of Sitka black-tailed deer. The conversion of uneven-aged, old-growth forests to even-aged, second-growth forests has generated concern about the future carrying capacity of the habitat for deer, especially where snow accumulation is common on winter ranges. Even-aged, second-growth forests produce very little forage for black-tailed deer. Young (<20 years), open stands produce greater amounts of forage than do old-growth stands. Snow accumulates to greater depths in openings than in forest, however, and forage becomes unavailable to deer as it is buried in snow. Habitat quality for Sitka black-tailed deer must be viewed as an energy benefit-cost relation. Energy intake decreases and energy expenditure increases as snow depth increases. Habitats differ in their canopy characteristics and in the amount and kind of forage they produce. The relative qualities of habitats shift with changing snow conditions. An understanding of these dynamic relationships between deer and their habitat is essential for developing management objectives for deer habitat. The current theory is largely qualitative and lacks the ability to yield unambiguous, quantitative predictions. Research is needed to quantify the key relationships between forest canopy and understory production and snow interception, and between the metabolic requirements of deer and the nutritional quality of available forage.

Keywords: Wildlife habitat management, wildlife habitat, timber management, habitat selection, deer (black-tailed), Alaska (southeast).

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