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Composition of Diets Selected by Sitka Black-Tailed Deer on Channel Island, Central Southeast Alaska

Thomas A. Hanley, Michael P. Gillingham, and Katherine L. Parker[1]

Abstract

Composition of diets selected by tame but free-ranging deer in a natural forest environment was studied throughout a 24-month period and summarized by mean monthly percentage composition on the basis of dry-matter intake. A modification of the standard bite-count method of diet determination was used. All forages were identified by species and plant part (leaf, twig). Major forages comprising the diet were identified seasonally and considered in relation to their role in the nutritional ecology of the deer. Overall, a simple but consistent pattern was evident in the data. When green, leafy forages (herbs and shrub leaves) were available, they were consistently targeted by the foraging deer, but as they became less available in winter, and especially with their burial by snow, diet composition shifted to less digestible woody forages (shrub twigs and conifer foliage) supplemented with highly digestible arboreal lichens. Although a wide array of potential forages are available during the growing season, dietary options shrink to a narrow range of important evergreen forbs, a few ferns, shrub twigs, and lichens in winter.

Keywords: *Odocoileus hemionus sitkensis*, plant unit, habitat, food, browsing, grazing, dietary, dry-matter intake, understory vegetation, *Tsuga heterophylla*, *Picea sitchensis*, *Vaccinium*, *Alectoria sarmentosa*, *Lysichiton americanus*, *Dryopteris expansa*, *Cornus canadensis*, *Rubus pedatus*, *Coptis aspleniifolia*, *Tiarella trifoliata*.

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[1] **Thomas A. Hanley** is a research wildlife biologist, U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Forestry Sciences Laboratory, 11175 Auke Lake Way, Juneau, AK 99801. **Michael P. Gillingham** and **Katherine L. Parker** are professors, Natural Resources and Environmental Studies Institute, University of Northern British Columbia, 3333 University Way, Prince George, BC, Canada V2N 429.

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Introduction

Knowledge of diet composition is essential to understanding animal-habitat interactions because diet composition directly determines the nutritional quality of the animal's food intake, and it also determines the selective pressures an animal exerts on its potential food base. For herbivores, knowledge of diet composition can be used to identify specific plant species and parts from within the entire vegetation community that are most important to the animal's nutritional ecology and are most directly affected by herbivory. Diet composition for a given species of herbivore differs greatly, however, with differences in relative availabilities, innate palatabilities, and nutritional qualities of forages, all of which differ geographically, seasonally, and phenologically. Diet composition, therefore, tends to be most relevant at a local and time-specific scale. Nevertheless, it is only through many studies of diet composition that a broad, general picture of how animals relate to their environment through nutritional interactions can emerge for a given animal species within a given ecological region.

Diet composition for Sitka black-tailed deer (*Odocoileus hemionus sitkensis*) in the western hemlock–Sitka spruce (*Tsuga heterophylla–Picea sitchensis*[2]) forests of southeast Alaska has been studied by numerous investigators since the late 1950s (reviewed by Hanley 1984: table 2), although most of the early work consisted simply of lists of major forages identified in the rumen contents of harvested deer. More quantitative study began in the 1980s with studies of both rumen contents and fecal composition (determined microscopically by identification of plant fragments on the basis of their cell wall structure and other unique identifying features) expressed on a percentage ovendry-weight basis (Hanley et al. 1985, Hanley and McKendrick 1985, Lewis 1994, Pierce 1981). Although the dry-matter composition of rumen contents and feces can be determined more or less accurately for forages comprising the bulk of the sample collected, composition of neither rumen contents nor feces is assured to be directly related to composition of the diet that produced them. The principal problems are that plant species (and even tissues within a species) differ greatly in their recognizability after having been chewed and digested, and they differ greatly in their retention time in the rumen, their rate of digestion, and their overall dry-matter digestibility. The consequence is that easily identifiable and poorly digested species tend to be overestimated while poorly identifiable and highly digested species tend to be underestimated relative to the true composition of the diet. These problems have been well known for many years (Dearden et al.

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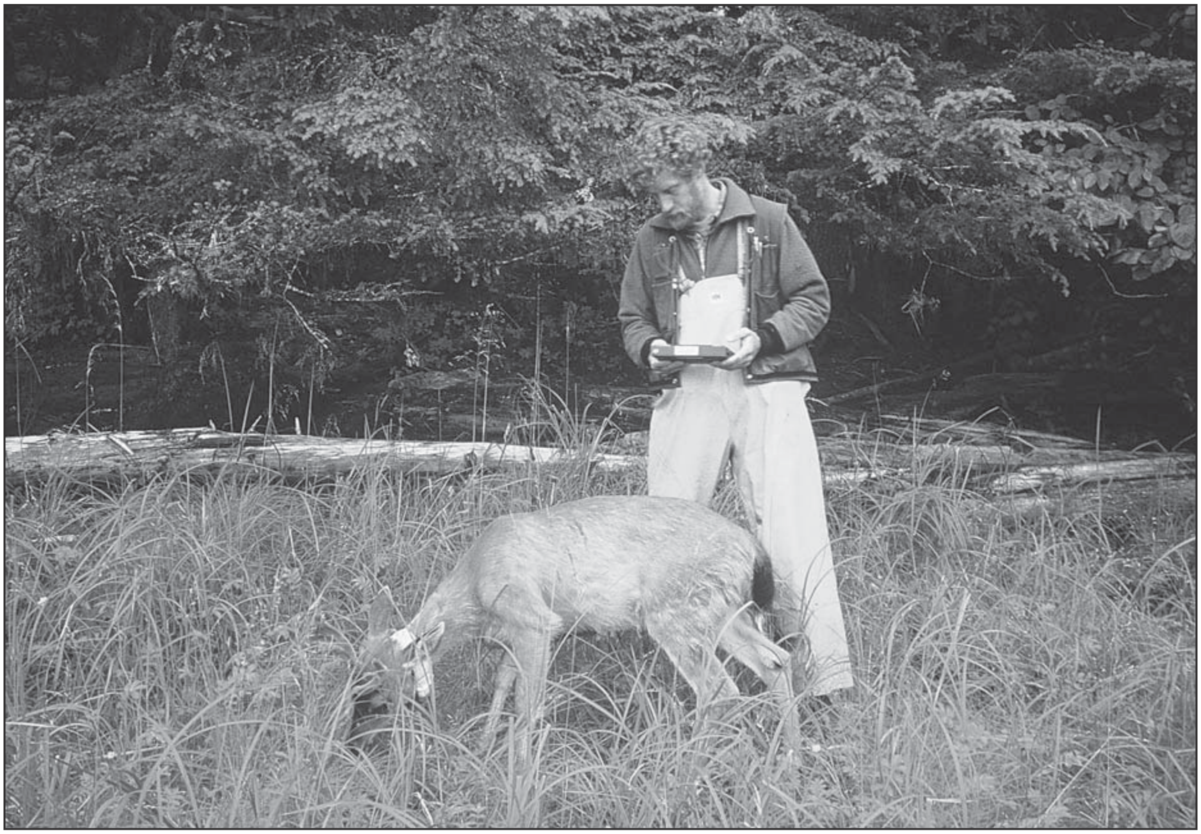
[2] See appendix for full scientific names, sources, and common names for all plants in this report.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M.P. Gillingham recording bites taken by a deer as it feeds on small forbs in a tidally influenced beach fringe habitat on Channel Island.

1975, Gaare et al. 1977, Havstad and Donart 1978, Slater and Jones 1971), and although partial solutions, including adjusting the results for dry-matter digestibility, have been suggested and used, the true composition of the actual diet can never really be determined by those techniques. For example, chewed and digested, young, highly digestible leaf tissue with few or no unique visually identifiable features will go unidentified particularly in the feces, no matter what its “correction factor” might be, yet that tissue might be some of the most nutritiously important in the diet.

In 1989 and 1990 (October 1988 through September 1990), a unique, intensive study of the nutritional ecology of Sitka black-tailed deer was conducted on Channel Island, near Wrangell, Alaska (Parker et al. 1999). Its primary purpose was to field test theory and hypotheses derived from independent studies of nutritional processes determining protein and energy balance of black-tailed deer in forest environments. The study involved closely monitoring the year-around activity, dietary intake, energy expenditure, and changes in body weight and composition of tame but free-ranging deer living without supplemental food on the island. Accurate determination of the true dry-matter composition of the diets selected by those deer was essential for the success of the study. Indeed, it was one of the principal reasons that tame deer were needed. The technique that was used involved identifying, counting, and tracking virtually all bites taken by animals under close observation by an observer while the animals were going about their usual daily activities (Parker et al. 1993a).

The data on diet composition from the Channel Island study are unusual and especially valuable in several respects: (1) they provide accurate estimates of actual dietary intake (not rumen or fecal composition); (2) observers were able to see plants and plant parts eaten that would never have been observed or identified in any other way; and (3) the data were obtained for every month over a full 2-year cycle. Although the results were used in many analyses and published reports from the study (e.g., Gillingham et al. 1997, 2001; Parker et al. 1993b, 1996, 1999), they were never published at the species level of diet composition, except in two composite figures identifying only a few of the most dominant species and major forage groups (figs. 5 and 8 in Parker et al. 1999). More recently, the need for more specific data on diet composition has become evident (e.g., in some aspects of habitat modeling—Hanley et al. 2012), and the value of those unique, highly accurate results from the Channel Island study has increased. Therefore, our purpose in this report is to provide a summary of those data at the species-specific and plant-part (leaves, twigs) levels of detail.

Methods

Study Area and Animals

The study was conducted on Channel Island (56° 22’ N latitude, 132° 10’ W longitude), a completely forested island of about 65 ha, approximately 20 km southeast of the town of Wrangell in central-southeast Alaska. Elevation ranged from 0 to about 125 m above mean sea level. Forest overstory was a mixture of old-growth western hemlock–Sitka spruce and variously disturbed younger stands resulting from windthrow and some old hand-logged sites. Understory included virtually all the major understory species typical of the region with the exception of a notable few such as salal (*Gaultheria shallon*), willows (*Salix* spp.), and cedars (*Thuja plicata*, *Callitropsis nootkatensis*). The vegetation occurred within three major associations or community types, named after their dominant species: blueberry-spreading woodfern (*Vaccinium ovalifolium–Dryopteris expansa*); skunkcabbage (*Lysichiton americanus*); and devilsclub (*Oplopanax horridus*). Additionally, there was an open “beach” habitat that rimmed the southeasterly edges of the island and was subject to occasional inundation by seasonally high tides; tidal flood was sufficient to exclude trees but seldom enough to allow a species-rich wetland flora to persist (see Parker et al. 1999 for more details of the vegetation, including a vegetation map and measures of seasonal availability). No resident deer were believed to inhabit Channel Island at the time the study began, and the study animals were the only deer known to inhabit the island during the study, although an occasional transient wild deer did come and go. Therefore, the vegetation of the island was virtually ungrazed before the study, and it remained lightly to moderately grazed during the study.

The study animals were nine Sitka black-tailed deer (two males and two females born in 1987, and two males and three females born in 1988). All were either born in a captive animal facility in Juneau, Alaska, or captured in the wild, separated from their mothers shortly after birth and transported to a small island next to Channel Island where they were bottle-raised and then weaned onto the natural vegetation of Channel Island (Parker et al. 1999). This hand-rearing technique imprinted the deer on their human handlers so they accepted the handlers without fear or concern throughout the study. The handlers were always able to work at very close proximity to the deer (e.g., within 0.5 m if desirable) without disturbing them. The technique had the disadvantage of the deer not learning from their mothers, but all nine deer quickly adjusted to the Channel Island vegetation and were able to select diets that adequately met their nutritional needs for maintenance, growth, and even reproduction (four singletons and two sets of twins were produced by the five females during the 2 years of data collection). Other studies have shown that hand-reared animals usually consume the same foods as maternally raised ones (Olsen-Rutz and Urness 1987, Spalinger et al. 1997). All deer utilized the entire island throughout the study. They all had seemingly unlimited access to all of the major forage species.

Diet Composition

Data were collected for the full 2-year period of October 1988 through September 1990. A unique technique for estimating food intake was developed and field-tested specifically for this study (Parker et al. 1993a). It was a modification of the conventional bite-count method of studying dietary intake of tame deer (Wallmo and Neff 1970) and consisted of defining a “plant unit” for each and every plant species and plant part (leaf, twig), where the plant unit was defined as an average-size piece of tissue commonly eaten by the deer, and intake was recorded in plant units instead of simply bite counts. In the case of small to medium-size leaves, the plant unit was often average leaf size; for large leaves (e.g., skunkcabbage), it was a square of specified size, about average mouth width of the deer. A two-dimensional template of the plant unit was made for each forage species or forage species of comparable size, and template sizes were memorized by the observers. Forage composition and intake rate were determined while observing foraging deer by counting and immediately recording (by plant species code in a portable data logger) the number of plant units of each forage consumed as it occurred. Representative plant units of all available forages were routinely collected, weighed, oven dried and reweighed throughout the study, thereby providing a basis for converting units consumed into both fresh and ovendry (100 °C) weights. This plant-unit technique worked well in the Channel Island communities of easily identifiable forbs and shrubs. Tests of the technique, comparing estimated weights of hand-harvested samples of plant material with actual weights, yielded an average correlation coefficient (*r*) of 0.985 (range of 0.970 to 1.00, with N ranging from 7 to 284) for 21 forages of widely varying size and form (Parker et al. 1993a). Throughout the study and this report, we differentiate between leaf and twig plant parts of the same species because they differ greatly in their nutritional value as forages for deer.

Individual animals were randomly selected for detailed study of their activity (including foraging) during 2- to 8-hour periods every several days throughout the 24 months of study. Although some activity trials occurred at night, only results from daytime trials are included in this report. Average diet composition and intake were determined for each of the animals on a monthly basis (see Parker et al. 1999 for details). Here we are concerned only with diet composition on an ovendry-weight basis, averaged across all animals each month.

Results and Discussion

Major Species and Plant Parts

Rather than presenting the raw monthly data for all plant species consumed in each of 24 months, we have summarized the results in terms of seasonal ranges in mean monthly diet composition for the four seasons of spring (April and May), summer (June, July, and August), fall (September, October, and November), and winter (December, January, February, and March) (table 1). Specific values of monthly means are not so informative, as they mainly reflect very local circumstances. But ranges of values, by major season, are informative because the range provides a more general description relative to seasonal variation, and the seasonal grouping of months provides a meaningful pooling of major environmental differences affecting both availability and nutritional quality of the forage resources. Note that the seasons we defined are not of equal length. Spring is the period of new greenup and early, rapid growth of previously dormant vegetation; summer is the period of maximum biomass and phenological maturation of most forages; fall is the period of onset of seasonal senescence, withdrawal of reserves from leaves to storage organs, leaf-drop and winter senescence, but mostly frost- and snow-free conditions under forest canopies at sea level; and winter is the period of leafless deciduous plants, full winter dormancy, and frequently frozen or snow-covered ground.

Over the course of the study, the deer ate at least a small amount of virtually all plant species occurring on the island, including even a few that were available only after washing ashore (Parker et al. 1999). Some forages were eaten only sparingly, perhaps as a taste or simply because of a desire for dietary diversity. Such rarely eaten species may not have been encountered during the diet-composition observations.

Overall, diets in spring, summer, and fall were highly diverse, with few species comprising large proportions of the diet (table 1). Forages that were eaten most were bunchberry (*Cornus canadensis*), false lily of the valley (*Maianthemum dilatatum*), skunkcabbage, Pacific silverweed (*Argentina egedii*), spreading woodfern, deer fern (*Blechnum spicant*), sedge (*Carex* spp.), rusty menziesia (*Menziesia ferruginea*) leaves, devilsclub leaves, blueberry leaves and twigs, western hemlock current annual growth (leaves and twigs together), Sitka alder (*Alnus viridis*) leaves, crabapple (*Malus fusca*) leaves, mushrooms, and witch's hair lichen (*Alectoria sarmentosa*), each of which constituted more than 10 percent of the diet in at least one month. Skunkcabbage, spreading woodfern, deer fern, menziesia leaves, and blueberry leaves and twigs were the dietary dominants (each >25 percent at some time), with skunkcabbage reaching as high as 49 percent of the diet in June of 1989.

Diets were much less diverse in winter, when forage availability was much reduced by both phenology (deciduousness) and burial by snow. Most of the summer forages in southeast Alaska are deciduous so are simply not present in winter, and Sitka black-tailed deer do not dig through snow for forage, so any food buried by snow is not available to them. Forages that constituted major proportions of the winter diet were bunchberry, spreading woodfern rhizomes, dead leaves of sedge, blueberry twigs, red huckleberry (*Vaccinium parvifolium*) twigs, western hemlock current annual growth, rockweed alga (*Fucus furcatus*), and witch's hair lichen, all of which comprised at least 10 percent of the diet in at least one month (table 1). Blueberry and witch's hair lichen were the most dominant forages then (each reaching 30 to 32 percent, respectively, at some time).

However, data on diet composition alone do not provide measures of relative importance of the various forages to deer because they are strongly affected by relative availabilities and do not include nutritional value. The most highly nutritious forages are often relatively rare on the landscape and so cannot be eaten in great quantities, whereas forages of marginal quality are often very abundant and may be eaten as simply a matter of last recourse. For example, in winter, the evergreen forbs bunchberry, five-leaved bramble, fern-leaf goldthread (*Coptis aspleniifolia*),

Table 1—Seasonal diet composition (percentage dry-matter intake) of black-tailed deer diets during the 24 consecutive months of observation

Forage class and species	Spring (April–May)	Summer (June–Aug.)	Fall (Sept.–Nov.)	Winter (Dec.–March)
		Percentage dry-matter intake		
Forbs:				
Achillea millefolium	t	t–1	0–1	0
Argentina egedii	t–1	1–10	0–3	0
Coptis aspleniifolia	0–1	t	t–8	t–4
Cornus canadensis	t–2	t–2	3–17	t–11
Equisetum arvense	0–5	t–1	0–t	0
Glaux maritima	0–t	t–2	0–t	0
Lysichiton americanus	6–33	14–49	3–22	0–8
Maianthemum dilatatum	3–21	1–10	t–1	0–t
Plantago macrocarpa	0–t	2–4	0–t	0
Plantago maritima	0–6	t	0–t	0–t
Rubus pedatus	t–1	t	t–8	t–5
Streptopus amplexifolius	t–4	t–3	0–t	0
Streptopus streptopoides	t–7	t–2	0–t	0–t
Tiarella trifoliata	0–t	t	t–3	0–2
Total forbs	**31–52**[a]	**38–74**	**14–51**	**t–24**
Ferns:				
Athyrium filix-femina	3–7	t–4	0–t	0–t
Blechnum spicant	0–1	t	0–28	0–8
Dryopteris expansa	t–26	t–2	1–31	t–37
Polypodium glycyrrhiza	0–t	0–t	0–3	0–2
Total ferns	**4–31**	**2–5**	**2–35**	**1–43**
Graminoids:				
Carex spp.	1–18	t–3	0–t	0–10
Deschampsia cespitosa	t–3	t–1	0–t	0–3
Elymus arenarius	t–2	0–t	0–t	0–6
Total graminoids	**5–21**	**1–4**	**0–t**	**0–10**
Shrub leaves:				
Menziesia ferruginea	0–t	1–23	0–29	0–t
Oplopanax horridus	0–4	6–14	t–10	0–t
Rubus spectabilis	t–1	t	t–3	0–t
Vaccinium ovalifolium[b]	t–26	t–8	t–3	0–t
Vaccinium parvifolium	0–t	t	t–3	0–2
Vaccinium species[c]	0–t	t	t–3	t–2
Total shrub leaves	**t–33**	**16–40**	**4–45**	**t–3**
Shrub twigs:				
Vaccinium ovalifolium[b]	0–27	0	0–t	2–30
Vaccinium parvifolium	0–t	0	0–t	2–23
Total shrub twigs	**0–27**	**0**	**0–t**	**4–52**
Trees:				
Alnus viridis leaves	t–2	2–10	0–4	0–4
Malus fusca leaves	0–3	t–2	t–21	0–t
Tsuga heterophylla CAG[d]	0–3	0–t	0–10	5–16
Total trees	**1–5**	**2–11**	**3–23**	**8–18**

Table 1—Seasonal diet composition (percentage dry-matter intake) of black-tailed deer diets during the 24 consecutive months of observation (continued)

Forage class and species	Spring (April–May)	Summer (June–Aug.)	Fall (Sept.–Nov.)	Winter (Dec.–March)
	Percentage dry-matter intake			
Other:[e]				
Alectoria sarmentosa [f]	t–10	t–1	t–15	8–32
Fucus furcatus	0–t	0–t	0–t	t–15
Lobaria spp.	0–t	0–t	0–1	t–6
Mushrooms	0	0–12	4–23	0–3
Peltigera spp.	0–t	0–t	0–t	0–1

Note: Values are ranges of monthly means, summarized by four seasons (spring, summer, fall, winter). Only forages that constituted at least 1 percent of mean dietary dry-matter intake during at least one month are included in the table. t = trace = >0 but <1 percent. See appendix for full scientific nomenclature and common names.

[a] "Total" values are the range of monthly totals; they are not a sum of data in the column above them.

[b] Includes *Vaccinium alaskaense*, which hybridizes with *V. ovalifolium*.

[c] Evergreen, decumbent, sexually immature form of *V. alaskaense*, *V. ovalifolium*, and *V. parvifolium*.

[d] CAG = current annual growth (current year's leaves and twigs together).

[e] Additional forages that were observed to be consumed but never constituted at least 1 percentage of the mean monthly dry-matter intake in at least one month included the following (with season in parentheses—spring, Sp; summer, Su; fall, F; winter, W):

Forbs—*Angelica lucida* (Sp, Su, F, W), *Aster* species (Su, F), *Castilleja hyperborea* (Sp, Su, F), *Clintonia uniflora* (Sp, Su, F, W), *Cochlearia groenlandica* (Su, F), *Conioselinum gmelinii* (Sp, Su, F), *Dodecatheon pulchellum* (Sp, Su), *Epilobium* species (Su), *Fragaria chiloensis* (Sp, Su, F), *Fritillaria camschatcensis* (Sp, Su), *Galium trifidum* (Su, F), *Heracleum maximum* (Su), *Lathyrus japonicus* (Sp, Su, F), *Listera cordata* (Sp, Su, F, W), *Lupinus nootkatensis* (Sp, Su, F), *Moneses uniflora* (Sp, Su, F, W), *Osmorhiza* species (Sp), *Prenanthes alba* (Sp, Su, F, W), *Ranunculus occidentalis* (Sp, Su, F), *Rumex* species (Su), *Trifolium* species (Sp), *Veratrum album* (Su), *Viola glabella* (Sp, Su, F);
Ferns—*Gymnocarpium dryopteris* (Sp, Su, F, W);
Graminoids—*Hordeum brachyantherum* (Sp, Su, F);
Shrub leaves—*Cornus sericea* (Su, F), *Ribes laxiflorum* (Sp, Su, F), *Ribes* species (Sp, Su, F), *Rubus parviflorus* (Sp, Su, F, W), *Sambucus racemosa* (Sp, Su, F, W), *Viburnum edule* (Su);
Shrub twigs—*Menziesia ferruginea* (F, W);
Trees—*Callitropsis nootkatensis* (W), *Picea sitchensis* (Sp, Su, F, W), *Sorbus aucuparia* (Su);
Other—*Lycopodium* species (F,W), *Marchantiophyta* (Sp), moss species (Su, F).

[f] Includes *Usnea* species that looks very similar to the more common *A. sarmentosa*.

and to a lesser degree, foamflower (*Tiarella trifoliata*) are among the most nutritious (Parker et al. 1999) and palatable forages, but they are very low growing and are among the first forages to be buried by snow. Their relatively low composition in the diet during winter (table 1) does not indicate a low importance; it indicates a low availability. In fact, those forbs are so important that their availability during snow-free conditions plays a major role in meeting the overall winter nutritional requirements for survival of deer in these forests (Parker et al. 1999). On the other hand, blueberry twigs are a marginally satisfactory winter forage in terms of their nutritional quality (Parker et al. 1999), but they are often the only nutritionally adequate forage rising through a snowpack. In their case, their high proportion of the diet does indicate relatively high importance, but only because of the relative unavailability of better forages. An understanding of the relative **importance** of any given forage, therefore, requires consideration of both its availability and its nutritional quality in relation to those of all other forages in the habitat at the same time. It requires either detailed study (e.g., like that of Parker et al. 1999) or analysis within a nutritionally based model (e.g., like that of Hanley et al. 2012).

Some of the forages identified as major dietary components (above) were eaten only at certain times or under certain circumstances, and their apparent high use within a season is an artifact of relatively high use at one specific time. For example, the use of alder and crabapple leaves was high only at their time of early senescence (alder in late August) and leaf-fall (crabapple in September). At other times, these two species were eaten only occasionally while green during the growing season or as dead leaves in winter. Similarly, sedges were a large dietary component in spring when they were young, fast-growing, succulent, and highly digestible (reaching a peak at 18 percent in May 1989), but they were virtually ignored at other times, except for heavy use (10 percent) in February 1990 during the deepest snow of the study when they provided one of the few alternatives to blueberry twigs and western hemlock foliage. The sedge leaves were dead then, but they occurred in the beach habitat where the snow was melted by tidal flood, and dead sedge leaves were the only “leafy” material available. That was also the same time that rockweed alga (another beach species of very low nutritional value–Hanley and McKendrick 1983, Parker et al. 1999) reached its high of 15-percent diet composition. At times and circumstances such as that, almost any available forage might be eaten just for variety; the spike in diet composition says virtually nothing about value or importance.

Many of the forbs in table 1 occurred in the beach habitat and are not typical of upland forest habitats. They often seemed to be eaten as simply an addition for dietary diversity, although we cannot know that for certain. In any case, their dietary roles were mainly an artifact of habitat and vegetation circumstances of Channel Island; they do not reflect broader patterns of diet composition of deer in forest habitats of the region, nor are they necessary foods for deer of the region. Other, common forest forbs could easily take their place.

Several new, important insights were gained in this study, and we believe they are likely to be generally true throughout the region. They involve specifically targeted plant tissues that came as a surprise to us or plant species or amounts that exceeded our expectations. Perhaps most surprising was the role that spreading woodfern played in the seasonal diets. Spreading woodfern is a common species widespread through many forest habitats of the region, and it was known from previous studies to be a fairly common dietary component for black-tailed deer, having been found frequently in both rumen contents and feces. However, only by direct observation was it possible to identify that different parts of the plant are eaten at different times of the year and that the plant is specifically targeted by deer in both the shoulder seasons of spring and fall. In early spring as the snow retreats and deer are in their most depleted body condition (Parker et al. 1999), spreading woodfern becomes available before most other species leaf out, and deer target the fern's fiddlehead still buried in the moss or duff of the forest floor. Timing of spring is an especially critical time for deer, both for surviving winter and for the nutritional demands of a gestating fawn; and fiddleheads of spreading woodfern are highly nutritious then (Parker et al. 1999). As summer progresses, deer consume the fronds of spreading woodfern, but only occasionally (table 1) and not importantly. However, in late fall after leaf fall of blueberry and other deciduous forage but before the forest floor freezes, deer actively target the rhizomes of the fern, buried in the forest floor but clearly evident because of the dead fronds on the ground (Gillingham et al. 2000); that activity carries into winter, too, but only when the ground surface is not frozen or snow covered. Spreading woodfern, therefore, again becomes an important forage because the rhizomes are a large bundle providing energy and protein at a time when other highly digestible forages have become mostly unavailable. Before the Channel Island study, the targeting and relative importance of spreading woodfern fiddleheads and rhizomes had never been noticed, or at least reported.

Similarly, skunkcabbage is another critically important forage in early spring, especially before green-up of other forages. It is usually the first plant to break forth from the ground surface, sometimes even through still-frozen ground (e.g., in March, table 1), and deer actively seek the bright yellow buds. Skunkcabbage is always very highly digestible and very protein-rich (Hanley and McKendrick 1983, Parker et al. 1999), but especially so in early spring at the very time that other forage resources are at their worst (Hanley and McKendrick 1985, Parker et al. 1999). Although skunkcabbage has long been known to be very important to deer then and also as a significant diet component throughout summer, it was surprising to see exactly how strong a diet component it could be during summer—reaching as high as 49 percent of dry-matter intake. Diet composition that high was surprising because skunkcabbage is such an extremely wet forage (ovendry weights are usually less than 10 percent of wet weights). Also, because of its very high dry-matter digestibility (e.g., 87 percent in spring, 76 percent in summer—Hanley and McKendrick 1983), it has been difficult to accurately estimate the true diet composition of skunkcabbage from rumen or fecal samples, even with adjustments for dry-matter digestibility. The very large leaf sizes, however, enable deer to have very high intake rates while eating it. Skunkcabbage was targeted by deer throughout the growing season on Channel Island and was the only species that noticeably suffered an obvious decline in its availability because of deer use (although it always remained widely available throughout the island).

False lily of the valley is a species that was known to be eaten by deer in spring and summer, but was never suspected of playing such a substantial role as 22 percent diet composition (in May 1990; 16 percent in May 1989). It is one of the early species to leaf-out in spring, and its leaves are especially succulent and digestible then (especially while still curled before unfurling in early May). We suspect that the leaf tissue is relatively lacking in uniquely identifiable morphological features then, which is the reason for its apparent underreporting in previous studies of rumen and fecal contents. On the other hand, we suspect that mushrooms, heavily targeted by the deer in the fall (and peaking at 23 percent of the diet in September 1990), have been underestimated in rumen and fecal studies because of their high digestibility, as their spores should be identifiable microscopically.

Another species that was eaten more than we expected was rusty menziesia. In both years of the study, consumption of leaves (but virtually never twigs) of this shrub peaked in late August to September (24 and 29 percent, 1989 and 1990, respectively), possibly reflecting their high availability combined with an elevated drive in the deer to maximize food intake for replenishing body reserves before winter. Daily dry-matter intake, especially among females recovering from the demands of fawn-rearing, peaked then, reaching as high as during peak lactation (fig. 8 in Parker et al. 1999). September is a month when both nutritional quality and available biomass of deciduous forages are declining rapidly with the onset of fall. Menziesia leaves retain their color and nutritional quality then (Hanley and McKendrick 1983); but perhaps more importantly, their growth in clumped whorls instead of isolated individuals makes them especially profitable food items in terms of dry-matter intake rate (Shipley and Spalinger 1992, Spalinger et al. 1988). Regardless of the reason, such high use of menziesia was surprising, and we suspect its use elsewhere might often be underestimated because of very low use of its twigs. Whereas browsed twigs are very obvious, missing leaves are not so obvious, especially in fall.

Similarly, but in an opposite pattern, we were surprised at the relatively low use of blueberry and red huckleberry leaves during summer. Red huckleberry leaves were seldom eaten year-around, but that might have largely reflected their relatively low availability on Channel Island. Oval-leaf blueberry, on the other hand, was the dominant shrub in most of the vegetation of the island, yet its leaves were eaten primarily in spring (up to 26 percent of the diet in May 1990) with less use later. Its twigs, too, were eaten then (up to 22 percent of the diet in April 1990) as they were recently emerged, rapidly growing, and at their peak nutritional value. In fact, dry-matter digestibility and digestible energy concentration not only peak in spring for blueberry (as for most other species, too), but leaves and twigs of blueberry have similar values then (Hanley and McKendrick 1983, Parker et al. 1999). By late August, though, digestible energy concentration of blueberry leaves was only 76 to 79 percent of that for menziesia leaves, and use of blueberry dropped to less than that of menziesia. The same pattern of high use of blueberry in early summer, shifting to highly digestible forbs and devilsclub leaves in midsummer, and greater use of menziesia than blueberry in late summer or fall has been observed elsewhere in the region, too (Hanley and McKendrick 1985). However, when shrub twigs became such an important dietary component in winter, then both blueberry and red huckleberry were the staple foods. Despite its much lower availability, huckleberry was avidly sought and eaten in almost similar proportion as blueberry then (up to 23 and 30 percent of the diet, respectively).

Several other species also were used less than we had expected. The four winter-evergreen forbs—bunchberry, fern-leaf goldthread, five-leaved bramble, and foamflower—comprised very small percentages of the diet in spring and summer (0 to 2 percent). It wasn’t until other, more succulent and digestible forbs became deciduous in the fall that the intake of these four species increased. Fall and snow-free conditions of early winter were the peak times of their use; they also were the times of their highest **relative** nutritional quality—relative to other forages.

Forage Classes and Temporal Pattern

Graphs of monthly changes in diet composition throughout the study (e.g., figs. 5 and 8 of Parker et al. 1999 or a plotting of totals for the major forage classes in table 1) are complex. However, if we view the forages in their most simple, nutritionally relevant classes of leafy material (herbs and shrub leaves), woody material (shrub twigs and conifer foliage), and highly digestible arboreal lichen (witch’s hair and beard lichens), then a simple, meaningful, and easily remembered pattern emerges (fig. 1). Furthermore, we are confident that this pattern is a consistent, highly predictable pattern for black-tailed deer throughout southeast Alaska because it is clearly related to relative availabilities and nutritional values of forages. Whenever green leafy material (highly digestible and nutritious) is available, it is avidly eaten; but when it is not available in winter, the diet shifts to woody browse supplemented with highly digestible lichen.

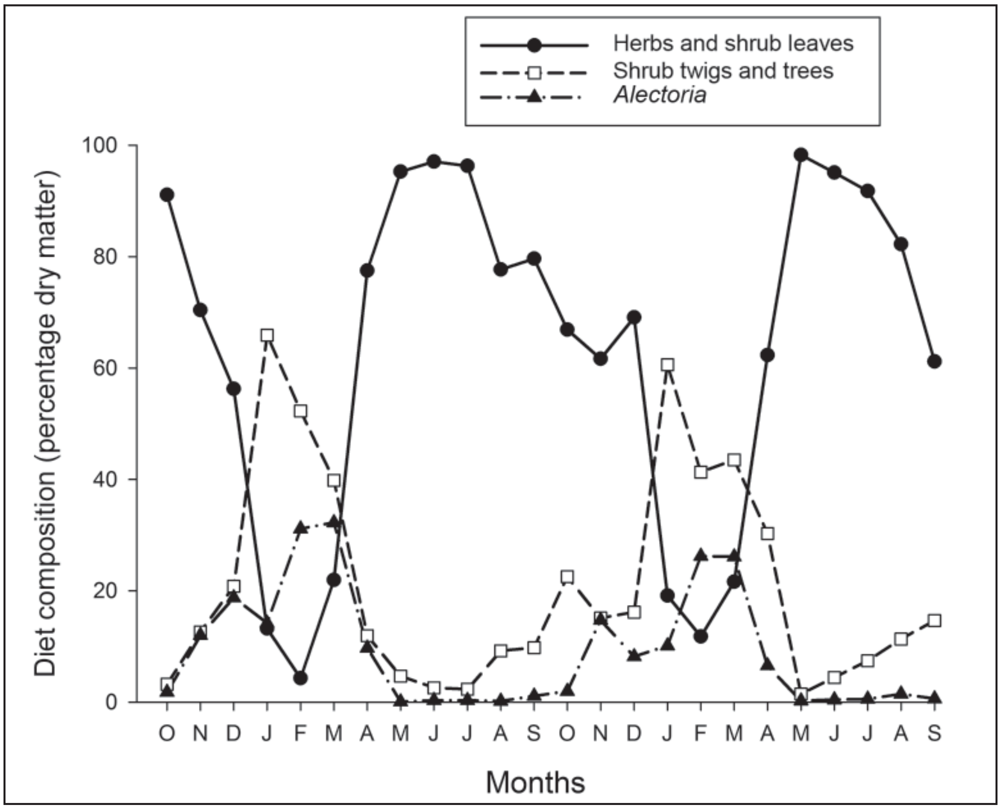

Figure 1—Mean monthly diet composition (percentage dry-matter intake) of black-tailed deer diets throughout the 24 consecutive months of observation, grouped by major forage classes of deciduous leaf material (herbs and shrub leaves), woody twigs and conifer foliage (shrub twigs and trees), and wind-blown arboreal lichen (*Alectoria*). "Herbs" are forbs, ferns, and graminoids.

The correlation (*r*) matrix for the data on diet composition during the 24 months of study (shown in fig. 1) is -0.950 for "Herbs and Shrub Leaves" with "Shrub Twigs and Trees"; -0.854 for "Herbs and Shrub Leaves" with "*Alectoria*"; and 0.713 for "Shrub Twigs and Trees" with "*Alectoria*." But more important than the *r* values, per se, is that the pattern and correlations make sense nutritionally.

A species-diverse diet of green leafy material provides a balanced diet that is rich in digestible energy, digestible protein, and other essential nutrients. Diet diversity is important in balancing both the nutritional needs of deer and the deleterious effects of tannins, nontannin phenolics, toxins, and other secondary compounds in plants (McArthur et al. 1993). However, during winter, especially with snow on the ground, green leafy material is not available, and shrub twigs (*Vaccinium* spp.) become the next best forage; yet alone, they are marginal at best for meeting the deer's requirement for digestible energy and might even be inadequate for sustained, over-winter survival. Therefore, the very highly digestible, energy-rich arboreal lichens are especially important then as a supplement to the energy-poor diet of woody twigs. For example, whereas the concentration of digestible energy was about 9.94 to 10.23 kJ/g for blueberry and red huckleberry twigs, respectively, in winter, that of witch's beard lichen was about 13.90 kJ/g (Parker et al. 1999). That 36 to 40 percent difference in digestible energy concentration is an enormous and very important difference to the winter energy budget of deer (Parker et al. 1999), especially if the deer are bulk-limited in their food intake while on the strongly woody diet. Although witch's hair and beard lichens contain such low concentrations of nitrogen that their digestible protein concentrations are actually negative numbers (-1.2 to -2.2 percent—Parker et al. 1999, Robbins 1987), protein is not a limiting factor for deer in winter because protein requirements are so low then and because the shrub component of the diet provides sufficient digestible protein (Parker et al. 1999). The importance of *Vaccinium* shrubs and witch's hair and beard lichens in winter diets of both Sitka and Columbian (*O.h. columbianus*) black-tailed deer in coastal Alaska and British Columbia, Canada, has been well known for many years (Hanley et al. 1989, Klein 1965, Rochelle 1980). On Channel Island, the deer commonly searched for and foraged on those wind-blown arboreal lichens during and after windstorms. Therefore, while the detailed, monthly data from the Channel Island study reflect many items that were very specific to only that study area at that specific time (e.g., the many wetland forbs in the beach habitat, the timing and amounts of snow, the heavy use of dead sedge leaves during the deepest snow[3]), the basic pattern of dietary change in relation to seasonal changes in forage availability (fig. 1) and many of the insights gained about key forage species and plant parts are very likely true throughout the range of Sitka black-tailed deer in southeast Alaska. Forage species will differ with habitat, especially in summer (e.g., use of alpine habitats by seasonally migratory deer), but the overall pattern of a diverse array of forbs dominating the summer diet, winter-evergreen forbs, *Vaccinium* shrubs, and wind-blown arboreal lichens being critically important in winter, and certain species such as skunkcabbage and spreading woodfern being highly sought in early spring captures much of the essential linkages among deer, their habitat, diet, and nutritional requirements.

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[3] Note that because sedge is a graminoid, and graminoids are included with "herbs" in figure 1, the sedge 10 percent diet composition in February, 1990, elevates the total herbs and shrub leaves disproportionately for that month. Herbs and shrub leaves are a high-quality forage class, but dead sedge leaves are very low quality.

English Equivalents

When you know:	Multiply by:	To get:
Centimeters (cm)	0.394	Inches
Meters (m)	3.28	Feet
Hectares (ha)	2.47	Acres
Square meters (m^2)	10.76	Square feet
Grams (g)	0.0352	Ounces
Kilograms (kg)	2.205	Pounds
Kilojoules (kJ)	0.2388	Kilocalories (kcal)
Kilojoules (kJ)	0.948	British thermal units (BTU)
Kilojoules per gram (kJ/g)	26.932	BTU/ounce

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Appendix: Scientific and Common Names of Plant Species in This Report[a]

Species	Common name
Achillea millefolium L.	Common yarrow
Alectoria sarmentosa (Ach.) Ach.	Witch's hair lichen
Alnus viridis (Chaix) DC. ssp. *sinuata* (Regel) Á. Löve & D. Löve	Sitka alder
Angelica lucida L.	Seacoast angelica
Argentina egedii (Wormsk.) Rydb. ssp. *egedii*	Pacific silverweed
Aster L. spp.	Aster
Athyrium filix-femina (L.) Roth	Common ladyfern
Blechnum spicant (L.) Sm.	Deer fern
Callitropsis nootkatensis (D. Don) Oerst. ex D.P. Little	Alaska cedar
Carex L. spp.	Sedge
Castilleja hyperborea Pennell	Northern Indian paintbrush
Clintonia uniflora (Menzies ex Schult. & Schult. f.) Kunth	Bridge's bonnet
Cochlearia groenlandica L.	Danish scurvygrass
Conioselinum gmelinii (Cham. & Schltdl.) Steud.	Pacific hemlockparsley
Coptis aspleniifolia Salisb.	Fernleaf goldthread
Cornus canadensis L.	Bunchberry dogwood
Cornus sericea L. ssp. *sericea*	Redosier dogwood
Deschampsia cespitosa (L.) P. Beauv.	Tufted hairgrass
Dodecatheon pulchellum (Raf.) Merr.	Darkthroat shootingstar
Dryopteris expansa (C. Presl) Fraser-Jenkins & Jermy	Spreading woodfern
Elymus arenarius L. ssp. *mollis* (Trin.) Hultén	American dunegrass
Epilobium L. spp.	Willowherb
Equisetum arvense L.	Field horsetail
Fragaria chiloensis (L.) Mill.	Beach strawberry
Fritillaria camschatcensis (L.) Ker Gawl.	Kamchatka fritillary
Fucus furcatus Esper	Rockweed
Galium trifidum L.	Threepedal bedstraw
Gaultheria shallon Pursh	Salal
Glaux maritima L.	Sea milkwort
Gymnocarpium dryopteris (L.) Newman	Western oakfern
Heracleum maximum W. Bartram	Common cowparsnip
Hordeum brachyantherum Nevski	Meadow barley
Lathyrus japonicus Willd. var. *maritimus* (L.) Kartesz & Gandhi	Beach pea
Listera cordata (L.) R. Br.	Heartleaf twayblade
Lobaria (Schreb). species	Lung lichen

Appendix: Scientific and Common Names of Plant Species in This Report[a] (continued)

Species	Common name
Lupinus nootkatensis Donn ex Sims	Nootka lupine
Lycopodium L. spp.	Clubmoss
Lysichiton americanus Hultén & H. St. John	American skunkcabbage
Maianthemum dilatatum (Alph. Wood) A. Nelson & J.F. Macbr.	False lily of the valley
Malus fusca (Raf.) C.K. Schneid.	Oregon crabapple
Marchantiophyta, a division of bryophytes	Liverworts
Menziesia ferruginea Sm.	Rusty menziesia
Moneses uniflora (L.) A. Gray	Single delight
Oplopanax horridus (Sm.) Miq.	Devilsclub
Osmorhiza Raf. spp.	Sweetroot
Peltigera Willd.	Felt lichen
Picea sitchensis (Bong.) Carrière	Sitka spruce
Plantago macrocarpa Cham. & Schltdl.	Seashore plantain
Plantago maritima L.	Goose tongue
Polypodium glycyrrhiza D.C. Eaton	Licorice fern
Prenanthes alba L.	White rattlesnakeroot
Ranunculus occidentalis Nutt.	Western buttercup
Ribes laxiflorum Pursh	Trailing blackcurrent
Ribes L. spp.	Current
Rubus parviflorus Nutt.	Thimbleberry
Rubus pedatus Sm.	Five-leaved bramble
Rubus spectabilis Pursh	Salmonberry
Rumex L. spp.	Dock
Salix L. spp.	Willow
Sambucus racemosa L.	Red elderberry
Sorbus aucuparia L.	European mountain ash
Streptopus amplexifolius (L.) DC.	Claspleaf twistedstalk
Streptopus streptopoides (Ledeb.) Frye & Rigg	Small twistedstalk
Thuja plicata Donn ex D. Don	Western redcedar
Tiarella trifoliata L.	Threeleaf foamflower
Trifolium L. spp.	Clover
Tsuga heterophylla (Raf.) Sarg.	Western hemlock
Usnea Dill. ex Adans. spp.	Beard lichen
Vaccinium L. spp.	Blueberry
Vaccinium alaskaense Howell	Alaska blueberry

Appendix: Scientific and Common Names of Plant Species in This Report[a] (continued)

Species	Common name
Vaccinium ovalifolium Sm.	Oval-leaf blueberry
Vaccinium parvifolium Sm.	Red huckleberry
Veratrum album L.	White false hellebore
Viburnum edule (Michx.) Raf.	Squashberry
Viola glabella Nutt.	Pioneer violet

[a] Source of nomenclature is PLANTS database, http://plants.usda.gov/java/.

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