An accurate technique for estimating forage intake of tractable animals

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We selected an average-sized plant unit for each forage species commonly eaten by black-tailed deer in southeastern Alaska. Those units, which were used to establish species-specific templates, typically represented single or small compound leaves that were usually eaten in one bite. We also determined an average mass for each plant unit. Using visual estimation of plant units in the natural environment, we were able to accurately predict actual plant mass (all $r^2 \geq 0.94$). The technique is an accurate and reliable method for estimating both bite sizes and cumulative forage intake of tractable animals in forb- and shrub-dominated communities. It provides an estimate of dry or wet matter intake within a foraging period or specific habitat patch, relative to diet selection at the plant species level.

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Nous avons choisi une unité végétale de taille moyenne pour chaque espèce de plante couramment consommée par les Cerfs à queue noire dans le sud-est de l'Alaska. Ces unités qui ont servi à établir des étalons spécifiques à chaque espèce, représentent ordinairement des feuilles simples ou de petites feuilles composées habituellement consommées en une bouchée. Nous avons également déterminé la masse moyenne de chaque unité végétale. Par estimation visuelle des unités végétales en milieu naturel, nous avons pu prédire de façon précise la masse végétale réelle ($r^2 \geq 0{,}94$ dans tous les cas). Cette technique constitue une méthode exacte et fiable qui permet l'évaluation de la taille des bouchées aussi bien que de la consommation cumulative de brout chez des animaux que l'on peut suivre dans les communautés dominées par des plantes buissonneuses ou des herbes autres que les graminées. La méthode permet aussi une estimation de l'ingestion totale de matières sèches ou fraîches au cours d'une période de quête de nourriture ou dans une parcelle spécifique d'habitat, en fonction du choix des espèces particulières de plantes consommées.

[Traduit par la rédaction]

Introduction

The energetic and nutritional balance of species living in seasonally variable environments imposes ecological constraints on individuals and influences population responses to habitat. Forage intake is often a more sensitive variable than energy expenditure and the use of body reserves for maintaining that balance in free-ranging ungulates (Wickstrom et al. 1984; Fancy 1986). Food quality and quantity control growth rate, reproduction, lactation, and other measures of individual animal productivity (Trudell and White 1981); food intake and digestibility are major factors determining over-winter survival (Hobbs 1989). Food intake depends on animal requirements but is constrained further by biomass, growth form, bite size, spatial distribution, and quality of the forage (Trudell and White 1981; Hudson and Watkins 1986; Spalinger et al. 1988). Consequently, feeding is also the dominant activity in the time budgets of free-ranging ungulates (Bunnell and Gillingham 1985). Despite the importance of forage intake to ungulate ecology and management, accurately quantifying the daily plant intake of animals in the wild remains difficult, largely because of methodological limitations.

Five methods have been used typically to quantify forage intake. They include the use of bite counts, biomass changes at feeding sites, fecal ratios, mass changes, and fistulated animals.

(*i*) With the bite count technique the researcher mimics animal intake by clipping or handpicking simulated bites that represent bites ingested (Wallmo and Neff 1970; Hudson and Nietfeld 1985; Renecker and Hudson 1985; Hudson and Watkins 1986). Subsequent estimates of intake rate require an accurate measurement of bite rate, bite size, and total foraging time. The method is nonobtrusive, but is biased towards plant species that are easiest to see at a distance when observing wild animals and especially by subjectivity in determining bite size. The use of tame, tractable animals has helped identify selected species, plant parts, and the phenological stages of ingested plants (Crawford and Whelan 1973).

(*ii*) A less direct method includes feeding site techniques, such as the twig count method, which estimates the amount of browse removed on the basis of the diameter at the point of browsing after animals have foraged. With this method it may be difficult to discern among herbivore species, and the method is biased towards plants for which removal is easiest to detect.

(*iii*) The ratio technique is the calculation of fecal excretion divided by the indigestibility of the diet. The method requires accurate measures of fecal output, often determined by external or indigestible internal markers, and diet digestibility. Given that digestibility and fecal production can be accurately determined, marker methods allow for simultaneous estimates

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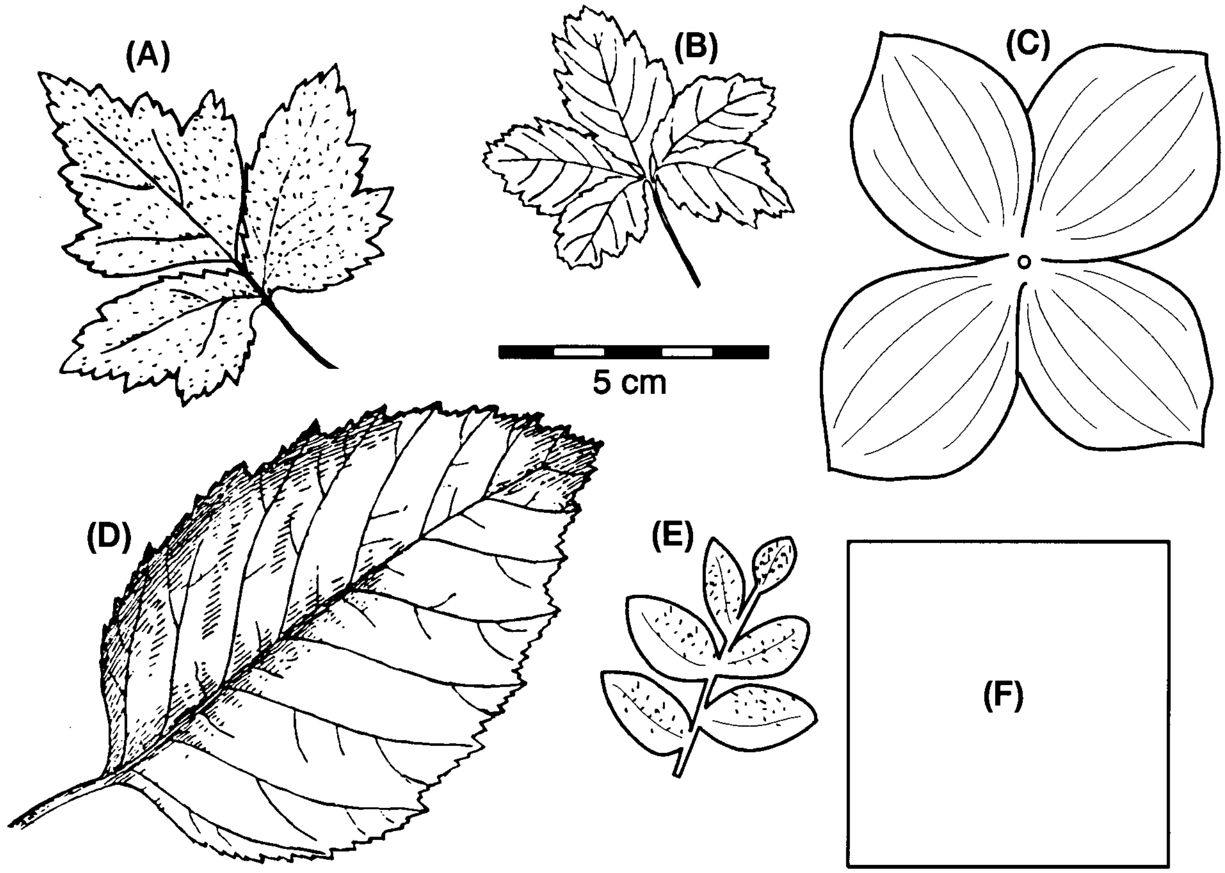

FIG. 1. Examples of plant unit templates representing one plant unit by species. Species are the following: (A) *Tiarella trifoliata*, (B) *Rubus pedatus*, (C) *Cornus canadensis*, (D) *Alnus sinuata*, (E) *Vaccinium parvifolium*, and (F) *Oplopanax horridum*.

of forage intake, passage rate, and digestive-tract fill, although quantifying the ingestion of biomass by species is not possible (Holleman and White 1989; Jiang and Hudson 1992).

The following two other common methods require tame, tractable individuals: (*iv*) measurements of short-term mass changes and (*v*) the use of oesophageally fistulated animals. The first can be limited by accessibility to a high-precision scale in the field; the second, while perhaps the best method available, requires intensive animal care and fistula maintenance (Whickstrom et al. 1984). One additional method to determine forage intake, which has not been frequently used, is the application of fallout radiocesium (Alldredge et al. 1974; Holleman et al. 1979). This technique can potentially determine the food selectivity of large herbivore populations if food resources are differentially labelled; however, intake rates and the concentration of label in the food resources must be assumed to be constant until an equilibrium body burden of radiocesium is attained (e.g., 80–90 days in reindeer; Holleman et al. 1979), when animals are sacrificed for isotope analysis.

We present a noninvasive technique for measuring forage intake of tractable free-ranging animals. The method was developed to determine intake by Sitka black-tailed deer (*Odocoileus hemionus sitkensis*), but it can be applied to other ungulates living in forb- or shrub-dominated habitats where eating behavior is clearly observable. Our method of 'plant units' is not constrained by time limitations, as are fecal markers, and allows for the determination of plant intake by species.

Material and methods

We developed the plant unit technique to estimate forage intake by tame Sitka black-tailed deer living on Channel Island. The study area, located 20 km southeast of Wrangell, Alaska (56°22′N, 132°10′W), was approximately 65 ha in size and entirely forested. Overstory consisted of western hemlock (*Tsuga heterophylla*) and Sitka spruce (*Picea sitchensis*). Understory vegetation was dominated by blueberry (*Vaccinium ovalifolium* and *Vaccinium alaskensis*), skunk cabbage (*Lysichiton americanum*), and devil's club (*Oplopanax horridum*).

We selected an average-sized plant unit for each forage species frequently ingested by the deer. Those units were typically single discrete leaves that were usually eaten in one bite, although small compound leaves were also represented by a single plant unit. The leaves were traced and cut into paper templates (Fig. 1). Because of the large size attained by leaves from *O. horridum* and *L. americanum*, we used an arbitrary bite unit represented by a square, 6 cm on a side. That was chosen because deer foraging on those species generally tended to tear and ingest the leaves in strips of approximately 6 cm. We memorized the size of each species-specific template and learned to recognize that size or portion of the plant unit in the natural environment. We later used the technique to estimate species-specific intake by the deer. For example, a leaf 50% larger in size than the species' template would represent 1.5 plant units; a leaf 50% smaller in size would be 0.5 plant units. We routinely weighed representative plant units for all species to determine wet mass, then dried those samples, and measured dry mass.

To quantify our accuracy in recognizing plant unit size, we estimated the plant size by species (e.g., 0.8 plant units of *Cornus canadensis*, or 1.5 units of *Rubus pedatus*), recorded the size on a portable computer programmed to calculate wet mass for each specific unit, and then picked the plant unit to determine actual mass

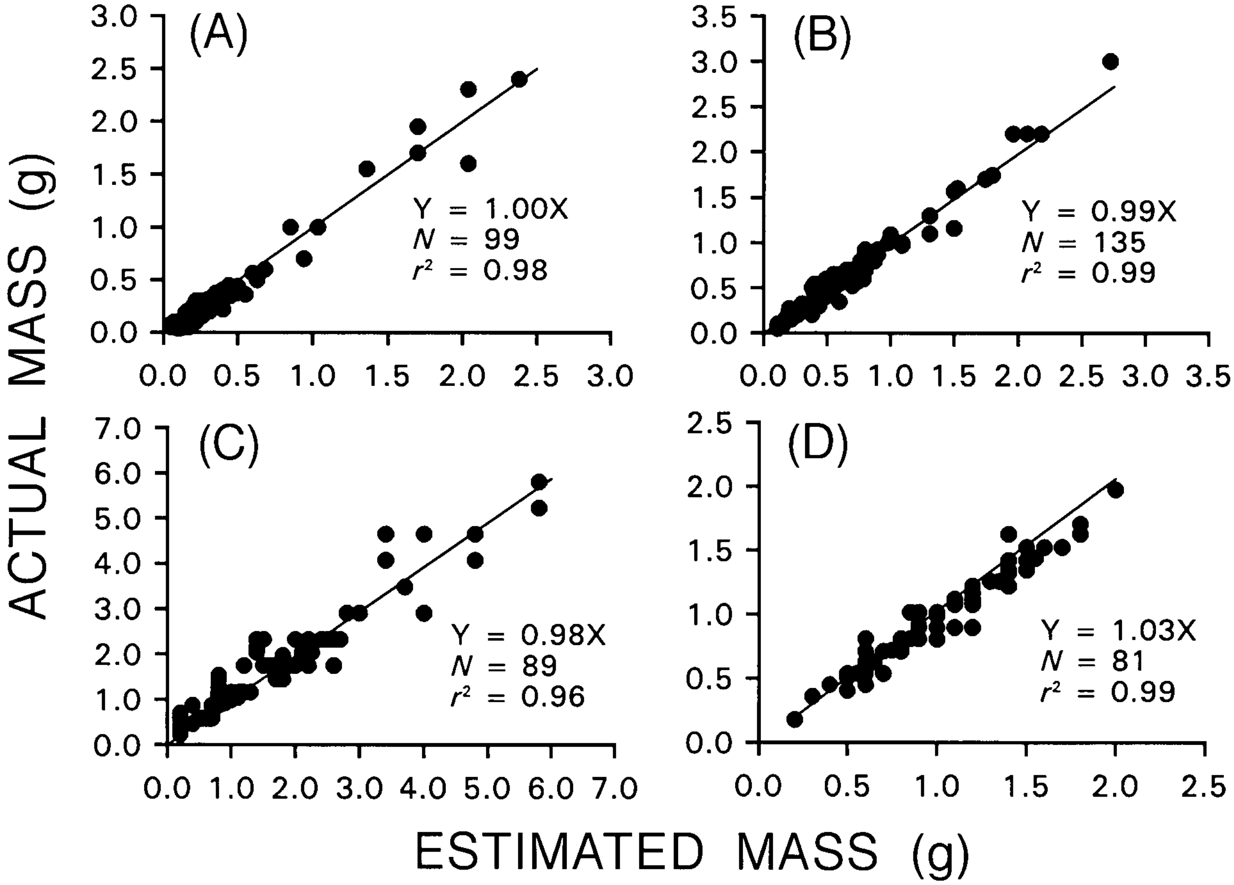

FIG. 2. Examples of actual versus visually estimated masses based on plant unit size for (A) *Tiarella trifoliata*, (B) *Vaccinium parvifolium*, (C) *Oplopanax horridum*, and (D) *Alnus sinuata*.

(Pesola scale, Switzerland). Validations of the technique lasting several hours were conducted without the observer knowing whether a previous sample was over- or under-estimated. We practiced learning to quickly recognize plant units in succession by estimating the mass of plants picked rapidly by another researcher to simulate animals foraging.

We assessed the accuracy of the technique by regressing actual plant masses on estimated masses based on plant units (PROC REG, SAS Institue Inc. 1987). All linear regressions were assumed to pass through the origin. We tested all slopes for significant differences from a slope of 1.0. We assumed a significance level of $\alpha = 0.05$.

Results and discussion

Plant masses based on visual estimates of plant unit size showed strong linear relationships with actual masses (Fig. 2). This applied to simple and compound leaves, for forbs and shrubs.

Plant masses estimated from plant units for forbs, shrubs, ferns, and a sedge commonly eaten by black-tailed deer on Channel Island were highly related to actual masses (Table 1). Slopes of the regressions were close to unity, estimates of goodness of fit (r^2) were high, and standard errors were low. With the exception of one species, *Coptis asplenifolia*, which is a pinnately compound forb with overlapping, sharply toothed leaves, all r^2 values exceeded 0.95; more than 75% were ≥ 0.97. Most of the slopes of the regressions were within a 3% error around a slope of 1.0. In the few cases in which slopes differed significantly from unity ($n = 4$), there was very low variation around the regression line causing slight differences in slopes to be significant; slope tests are inseparable from the overall fit of the data to the regression. For example, lower r^2 values may have resulted in slopes not different from unity. If we extrapolate the results of this validation to estimating intake by deer, forage intake would be underestimated by only 6% in the worst case when animals were selectively consuming *Maianthemum dilatatum* for extended periods of time. For generalist herbivores such as deer, however, errors in dry matter intake would be much smaller because of the mixed nature of their diet.

The plant unit technique allows for standardization among observers who learn to recognize a consistent plant unit size, the forage value of which can be assessed routinely for seasonal changes in mass and quality. The technique is highly repeatable, as indicated by the high r^2 values for the regressions between actual and estimated plant masses (Table 1) in our forb- and shrub-dominated habitats. Additional studies are necessary to determine how well the plant unit technique would work in grassland or tundra environments where it is more difficult to see how many shoots, blades, and stems are cropped. We determined the accuracy of estimating plant masses on the basis of plant units statically for rooted species and dynamically when a fellow researcher rapidly picked plants to simulate foraging by an animal. We have since used the technique to estimate the forage intake of tractable free-ranging deer (K.L. Parker and M.P. Gillingham, unpublished data). Because the accuracy of using plant units depends on the proximity of the observer to the foraging animal, the approach-

TABLE 1. Comparison of slopes and their standard errors, and percent variation explained by regressions for actual masses versus those estimated visually using the plant unit method for plant species commonly eaten by black-tailed deer

	Slope	SE	P (slope = 1)	r^2	n
Achillea millefolium	1.03	0.022	0.184	0.99	31
Alnus sinuata	1.03	0.009	0.001	0.99	81
Angelica lucida	1.03	0.018	0.121	0.99	43
Athyrium filix-femina	0.99	0.017	0.747	0.98	59
Carex spp.	1.03	0.013	0.085	1.00	7
Coptis asplenifolia	1.01	0.033	0.738	0.94	63
Cornus canadensis	0.98	0.027	0.546	0.95	67
Dryopteris dilatata	1.00	0.015	0.931	0.96	178
Ligusticum scoticum	1.00	0.015	0.925	0.99	36
Lysichiton americanum	0.96	0.009	0.000	0.98	284
Maianthemum dilatatum	0.94	0.010	0.000	0.97	243
Malus fusca	1.01	0.024	0.546	0.97	55
Menziesia ferruginea	1.02	0.025	0.399	0.99	25
Oplopanax horridum	0.98	0.020	0.345	0.96	89
Prenanthes alata	0.96	0.015	0.018	0.99	40
Ranunculus occidentalis	1.01	0.012	0.554	0.99	36
Rubus pedatus	0.97	0.018	0.117	0.97	91
Streptopus amplexifolius	0.97	0.018	0.124	0.98	50
Tiarella trifoliata	1.00	0.016	0.868	0.98	99
Vaccinium alaskaense	1.02	0.024	0.463	0.96	82
Vaccinium parvifolium	0.99	0.010	0.439	0.99	135

ability of the animal may limit use of the technique for some wild species.

Our data suggest that the plant unit technique can be used to provide accurate bite-by-bite estimates of forage intake. It has flexibility in that although the size of the template is fixed for a given species, the bite size taken by an animal is variable and can be estimated using plant units. In the case of large skunk cabbage leaves, deer tend to take bites that are larger than will fit in the mouth (much larger than the 6 × 6 cm plant unit), and feed the mass through the diastema directly to the molars (as in Shipley and Spalinger 1992). Therefore, bite size is not interchangeable with the term plant unit, but it can be determined from the plant unit. Plant units can also be used on a more cumulative basis over long periods of time. For example, in our deer research involving observations up to 8 h, we usually recorded a numerical code for the plant species eaten followed by the number of plant units eaten before the animal switched to another species or behavior (K.L. Parker and M.P. Gillingham, unpublished data). Hence, we noted forage intake by species rather than recording every bite cropped at a single instance. Total intake within a foraging bout was determined by summing the masses of all plant units eaten; intake rates were calculated from the forage mass consumed per unit time observed.

The plant unit technique has advantages over marker methods that necessitate averaging over long time periods and do not yield forage species-specific intakes. Esophageal fistulae methods are very useful in the short term, but are of less practical use for extended periods in the field because of the animal care and attention required. The strength of the plant unit technique, while requiring continual observations, is that it provides an estimate of dry or wet matter intake within a foraging period or within a specific habitat patch. It allows the opportunity to assess the dynamics of foraging ecology that involve diet selection at the plant species level and the efficiency of foraging within a bout.

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