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Biomass of Food Available to Beavers on Five Minnesota Shrubs

Richard R. Buech and David J. Rugg

The diet of beavers includes bark and leaves from woody vegetation (Jenkins and Busher 1979). Although bark is an important food year-round, beavers eat much foliage in summer (Svendsen 1980). In some habitats of northeastern Minnesota, beavers eat considerable bark and leaves from tall shrubs (Buech 1985). Presently, only graphical and tabular relations for *Populus tremuloides* Michx. and *Alnus* spp. (Aldous 1938, Stegeman 1954) and an equation for *Salix alba* (Nolet and Rosell 1994) are available in the literature for estimating food available to beavers on woody vegetation. Equations based on some dimension of the plant are generally easier to use, and offer an opportunity to include confidence intervals for predictions of biomass. Although published biomass-dimension equations are available for leaves of tall shrubs common to northeastern Minnesota (Parker and Schneider 1975, Connolly and Grigal 1983, Smith and Brand 1983, Buech and Rugg 1995), none have been published for bark. Therefore, we developed equations to estimate biomass of food available to beavers on five tall shrubs common to northeastern Minnesota.

METHODS

The Variables

Beavers eat both bark and leaves of tall shrubs. Because leaves are present only during the growing season, two estimates of available food are presented: "bark" (bark only, for use outside the growing season) and "total" (bark and leaves, for use during the growing season). Note that the term "bark" may include some woody material unavoidably consumed on small diameter twigs. This occurs because beavers debark stems to a point where the diameter is so small that they eat the entire twig, both wood and bark. We observed that beavers debark stems down to 5 mm outside diameter (od); smaller stem segments are entirely eaten. Thus, we considered "bark" to include bark only on stem segments greater than ≥ 5 mm and both wood and bark on stem segments < 5 mm od.

The literature provides some guidance for choosing a predictor variable to estimate biomass of woody vegetation components. Stem diameter (Ohmann *et al.* 1976) or stem diameter in conjunction with other variables (Ek 1979, Schmitt and Grigal 1981, Crow 1983, Jokela *et al.* 1986, Buech and Rugg 1995) has consistently provided good estimates of biomass. We chose stem diameter class as the predictor variable because it provides reasonable estimates (Ohmann *et al.* 1976, Buech and Rugg 1995) and because it can be rapidly measured in the field with the use of templates (Ohmann 1973). In fact, diameter class can be ocularly estimated by an experienced person and questionable stems can then be checked with templates.

Field and Laboratory Procedures

Biomass relations were determined for [<u>n</u> in brackets]: mountain maple (*Acer spicatum* Lam.) [60], green alder (*Alnus crispa* (Ait.) Pursh.) [95], speckled alder (*Alnus rugosa* (Du Roi) Spreng.) [124], juneberry (*Amelanchier* spp. Medic.) [61], and beaked hazel (*Corylus cornuta* Marsh.) [84]. Shrubs were collected during August and early September of 1979 and 1980 from stands 21 km southeast of Ely in Lake County, Minnesota, and processed as described by Buech and Rugg (1989). We measured stem diameter class at 15 cm above ground (in 12

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quarter-centimeter diameter classes, e.g., class 2 = stems 0.26-0.50 cm). We divided shrubs into the following components {component number in brackets}: leaves {1}, twig sections with od ≤5 mm {2}, bark {3}, and wood {4} components of twig sections with od >5 mm, deadwood {5}, and fruit {6}.

Data Analysis

The dependent variables were dry weight (dwt) of leaves {component 1}, "bark" {components 2 and 3}, and "total" {components 1, 2, and 3} beaver food. Biomass-diameter class relations were expressed in the raw scale using the allometric equation:

$$Y = \alpha_0 D^{\beta_1} \qquad [1]$$

where Y is biomass (g), and D is stem diameter class (1 to 12). Heterogeneity of variance was substantial, so the analyses were conducted and are reported here in the log-transformed scale (all references to "log-transform" indicate log base e):

$$\log Y = \beta_0 + \beta_1 * \log D \qquad [2]$$

where $\beta_0 = \log(\alpha_0)$. These linear models were used to assess choice of independent variables and models; coefficients of determination reported are adjusted R^2 values.

RESULTS AND DISCUSSION

The Equations

Parameter estimates and summary statistics are provided in table 1 for each variable by species and for all species combined. Fit of the allometric model was good; R^2 values ranged from 0.85 to 0.98. R^2 values for combined species models were generally the same or only slightly less than those for individual species models for both variables. This result is consistent with findings for other variables for the same species (Buech and Rugg 1989). It shows that generalized equations can provide reasonable estimates in instances where available resources preclude developing equations for local species.

Regressions for "bark" predict amount of bark on individual stems. Based on our equations, percent of total aboveground biomass considered to be bark differed among species and ranged from 7 to 29 percent for size class 1 to 17 to 20 percent for size class 12. In contrast, percent of total above-ground biomass for total food (including leaves) was similar among species and ranged from 100 percent for size class 1 down to about 40 percent for size class 12.

Using the Equations

The equations can be applied to predict biomass of available food from stem diameter class. Suppose an *Acer spicatum* shrub has a stem diameter of 1.34 cm at 15 cm above ground. This diameter would correspond to stem diameter class 6. To predict biomass of bark (g dwt) from stem diameter class, look up the values for $\hat{\beta}_0$ and $\hat{\beta}_1$ in table 1 for *Acer spicatum* and Bark, and substitute in equation [2]:

$$Y = -0.7189 + 2.3757 * (\log 6).$$

A hand calculator readily gives an answer of 3.5378 log g dwt of bark for this stem. A simple back-transformation provides the median biomass in the raw scale as 34.39 g. The mean biomass in the raw scale is calculated using the formula $E(Y) = \exp(\mu + 1/2\sigma^2)$ (Lindgren 1976), where μ is estimated by log Y, and the estimate for σ^2 is found in the MSE column of table 1. In this case, $E(Y) = \exp(3.5378 + 0.5*0.1305) = 36.71$ g.

Calculating the variance of this prediction is more involved (Draper and Smith 1981):

$$V(\log \hat{Y}) = \hat{\sigma}^2 + V(\hat{\beta}_0) + (\log D)^2 * V(\hat{\beta}_1) + 2*(\log D)*\mathrm{Cov}(\hat{\beta}_0, \hat{\beta}_1) \qquad [3]$$

For our example, this results in:

$$V(\log \hat{Y}) = 0.1305 + 0.01370 + (1.7918)^2 * 0.004153 + 2*1.7918*(-0.006917) = 0.1327.$$

Given the high R^2 for this model, it should be no surprise that the prediction variance is only 1.7 percent higher than the base MSE. This variance estimate can be used in conjunction with Student's t-tables to generate confidence intervals for predictions, probabilities of biomass being larger than some desired value, etc. Once the interval end-points have been calculated, a simple back-transformation will provide the appropriate interval in the raw scale, if desired.

Suppose you want to compute the variance of a predicted mean based on *m* new observations at log D=x, then the appropriate formula is (Draper and Smith 1981):

$$V(\log \hat{Y}) = \hat{\sigma}^2/m + V(\hat{\beta}_0) + x^2 * V(\hat{\beta}_1) + 2*x*Cov(\hat{\beta}_0, \hat{\beta}_1) \quad [4]$$

Comparison to Previous Estimates

Published biomass-dimension relations that predict food available to beavers (Aldous 1938, Stegeman 1954) assumed that beavers debark stems down to 12.7 mm od, but eat both bark and wood on smaller diameter stems. In contrast, we observed that beavers debark stems down to 5 mm od. Under our 5 mm od assumption, relations reported by Aldous (1938) and Stegeman (1954) overestimate food available to beavers. For example, Aldous' estimates for *Alnus* are roughly twice our estimates.

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Table 1.—*Regression statistics for predicting dry weight biomass (g) of food available to beavers on five tall shrubs. Parameters are from the relationship* $E(\log Y) = \beta_0 + \beta_1 * (\log D)$*, where D = stem diameter class at 15 cm above ground; logarithms are base e. The 12 stem diameter classes were 2.5 mm wide and covered the diameter range of 0 to 3 cm, e.g., size class 5 = stems >1.0 and ≤1.25 cm.*

Species	Food type	Parameter	Estimate	Var(β_i)	Cov(β_0, β_1)	MSE	R^2	n[1]
Acer spicatum	Leaves	β_0	-0.4233	2.594E-02				
		β_1	1.9820	7.865E-03	-1.310E-02	0.2471	0.96	60
	Bark	β_0	-0.7189	1.370E-02				
		β_1	2.3757	4.153E-03	-6.917E-03	0.1305	0.96	60
	Total food	β_0	0.1519	1.684E-02				
		β_1	2.1836	5.106E-03	-8.504E-03	0.1604	0.94	60
Alnus crispa	Leaves	β_0	-0.6333	2.380E-02				
		β_1	2.0302	7.565E-03	-1.271E-02	0.2298	0.85	94
	Bark	β_0	-0.7003	1.262E-02				
		β_1	2.5775	4.046E-03	-6.756E-03	0.1268	0.95	95
	Total food	β_0	-0.0922	1.417E-02				
		β_1	2.4349	4.544E-03	-7.588E-03	0.1424	0.93	95
Alnus rugosa	Leaves	β_0	-0.6015	1.387E-02				
		β_1	1.8909	4.209E-03	-7.027E-03	0.2583	0.88	121
	Bark	β_0	-0.8770	6.907E-03				
		β_1	2.5025	2.044E-03	-3.474E-03	0.1193	0.96	119
	Total food	β_0	-0.0195	6.421E-03				
		β_1	2.2502	1.926E-03	-3.233E-03	0.1172	0.96	118

(table 1 continued on next page)

(table 1 continued)

Species	Food type	Parameter	Estimate	Var(β_i)	Cov(β_0, β_1)	MSE	R^2	n[1]
Amelanchier spp.	Leaves	β_0	-0.9211	3.279E-02				
		β_1	1.9968	1.128E-02	-1.737E-02	0.3011	0.88	50
	Bark	β_0	-0.0016	5.084E-03				
		β_1	2.2678	1.520E-03	-2.552E-03	0.0488	0.98	61
	Total food	β_0	0.3388	5.697E-03				
		β_1	2.2257	1.959E-03	-3.019E-03	0.0523	0.98	50
Corylus cornuta	Leaves	β_0	-1.0671	1.712E-02				
		β_1	2.3366	7.671E-03	-1.027E-02	0.2804	0.90	83
	Bark	β_0	-0.9187	8.963E-03				
		β_1	2.6411	3.918E-03	-5.331E-03	0.1334	0.96	78
	Total food	β_0	-0.2355	8.420E-03				
		β_1	2.4908	3.688E-03	-5.019E-03	0.1256	0.96	79
All species combined	Leaves	β_0	-0.7216	4.449E-03				
		β_1	2.0311	1.484E-03	-2.358E-03	0.2875	0.87	408
	Bark	β_0	-0.6793	2.461E-03				
		β_1	2.4795	7.950E-04	-1.288E-03	0.1541	0.95	413
	Total food	β_0	0.0214	2.224E-03				
		β_1	2.3039	7.369E-04	-1.175E-03	0.1404	0.95	402

[1] *Variability in sample sizes (n) is due to missing data and deletion of outliers.*