Winter Diet of Snowshoe Hares in Managed Forests, Southwest Montana

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Abstract

We followed snowshoe hare tracks during winter months from 2000 through 2003 to locate feeding sites to study snowshoe hare *(Lepus america1111s)* diet in a portion of the Greater Yellowstone Ecosystem (GYE) near Gardiner, Montana. We observed browsing on 18 different forbs, shrubs, and trees, but 83 percent of the diet consisted of lodgepole pine *(Pinus contorta),* Douglas fir *(Pseudotsuga menzicsii),* and subalpine fir *(Abies lasiocarpa).* When we compared hare diet with plant availability in the different cover types within our study area, we found a significant correlation in only young regenerating stands of lodgepole pine. Plant availability greatly influenced hare diet as shown by a reduction in the number of different species being utilized by hares as winter progressed, and smaller plants became buried under accumulating snow pack. Hares also took advantage of fallen branches from mature trees laying on the snow pack, especially in more open cover types where food sources were less abundant.

Key words: *diet, Greater Yellowstone Ecosystem, Lepus americanus, lodgepole pine, snowshoe hare, winter*

Introduction

Researchers and managers have directed their attention towards mid-sized forest carnivores in recent years—in particular, the Canada lynx (*Lynx canadensis*). In 2000, lynx were listed as a threatened species in the contiguous United States under the Endangered Species Act. A more complete understanding of snowshoe hare ecology, including their diet, is needed (Ruggiero et al. 2000) due to its importance as a prey species of lynx as well as other mid-sized forest carnivores. Such an understanding applies especially at regional scales, e.g., the GYE, where a knowledge of snowshoe hare ecology had not been developed.

Snowshoe hare diets vary widely across their geographic range and among seasons within a specific area. Hares typically feed on succulent herbaceous vegetation during summer. In winter they browse on trees and shrubs (de Vos 1964, Wolff 1978). Although hares eat a wide variety of plants, including conifers and deciduous shrubs, they often show preference for certain species (de Vos 1964) that varies greatly among regions and depend on the local plant community (Hodges 2000). Wolff (1978) and others have noted that density and frequency of occurrence of plant species within different habitats greatly affect composition of snowshoe hare diets, but several studies have shown that, where present, pines are often the preferred coniferous winter browse (de Vos 1964, Pietz and Tester 1983).

Winter plant availability is greatly influenced by snow accumulation. Grasses, forbs, and small shrubs that are important components of the summer diet are often unavailable to hares during winter. High snow levels also allow hares to reach branches well above the ground that are typically unreachable during other periods of the year (de Vos 1964, Smith et al. 1988). During winter, snowshoe hares feed predominately on woody vegetation and can reach stems ≤ 50 cm above the snow surface (de Vos 1964, Smith et al.1988). Hares feed on woody plants by clipping small diameter twigs and needles or by removing bark on younger trees.

Although studies of snowshoe hare diet are fairly common across North America and Montana (Adams 1959, Malloy 2000, McKelvey et al.2002), relatively little work has been done within the GYE. Since substantial variation in snowshoe hare diet exists among locations, this study represents an opportunity to determine how snowshoe hare diet within a drainage in the northern portion of GYE compares to other populations in the Rocky Mountains.

During the winters of 1999-2003, we monitored snowshoe hare diet in an area heavily impacted by > 50 yrs of silvicultural treatment, including clear-cutting, selective harvesting, and precommercial thinning. Our study objective was to describe variability in hare diets among different cover types and winter months relative to food availability.

Study Area

This study was conducted in the Bear Creek drainage on the Gallatin National Forest northeast of Gardiner, Montana that encompassed ~ 11.7 km^2 (1172 ha) between Yellowstone National Park and the Absaroka-Beartooth Wilderness. For a more detailed description of the study area, see Zimmer et al. (2008). Average snow pack in March over the past 60 yrs on nearby Crevice Mountain (2560 m) was 99 cm (USDA 2003). Snow pack on the upper portion of the study area was very comparable to that observed on Crevice Mountain but lower elevations of the study area received considerably less snow.

Coniferous forests covered the majority of the study area. At elevations below 2280 m, Douglas fir was the dominant overstory species and covered 8 percent of the study area (Table 1). Lodgepole pine was the dominant species above 2280 m. We determined cover type proportions across the study area from a map developed for the cumulative effects model (CEM) by the Interagency Grizzly Bear Study Team (USDA 1990). This map, routinely used by biologists in the Yellowstone Ecosystem to identify habitat types, indicated that different successional stages of lodgepole pine forests covered 62 percent of the study area. Other cover types in the study area included Engelmann spruce (*Picea engelmannii*) and subalpine fir and mixed forest which covered 16 and 8 percent of the study area, respectively.

The forest understory was dominated by birch-leaved spiraea (*Spiraea betulifolia*) and snowberry (*Symphoricarpos albus*) at lower elevations, whereas higher elevations contained predominantly subalpine fir, whitebark pine (*Pinus albicaulis*), buffaloberry (*Shepherdia canadensis*) and twinberry (*Lonicera involucrata*). For this study, understory included all vegetation within ~ 4 m of the ground including lower branches of large trees as well as small trees, shrubs, and forbs.

Methods and Materials

Vegetation Availability

We used standard techniques outlined for Forest Service stand exams for timber management (USDA 1986, USDA 2000) to compare species composition and density within different cover types in our study area. We randomly selected 18 sites in each of the cover types. At each site, we established two concentric fixed-radius plots based on standard procedures for Forest Service stand exams. The first was a 3.6-m radius plot. For each live tree rooted within the circle, we determined species, height, diameter at breast height (DBH), height to canopy, canopy ratio, and canopy class. Height to canopy was measured from the ground to where the lowest live branches formed nearly a complete canopy around the tree. We defined canopy ratio as the proportion of total tree height that consisted of live canopy. Canopy class defined how each tree compared to other trees in the area: remnant, dominant, codominant, intermediate, or overtopped.

After all trees were classified, we established a 2.1-m radius plot from the same center point that was used for the 3.6-m radius plot. This plot was divided into two horizontal layers from the ground up to 1 m and from 1 m to 2 m. This provided us with estimates of plant availability in early winter (< 1 m snow depth) and availability during late winter (> 1 m snow depth). We estimated percent canopy cover by species for all trees and shrubs that had canopy within either layer. We did not attempt to quantify herbaceous cover within the plots because most grasses and forbs were buried in snow and served as a minor food source for hares during winter months.

Food Habits

Several methods have been used to look at snowshoe hare diets including stomach content analysis, scat analysis, observing hares, feeding trials, tracking to locate feeding sites, and vegetation monitoring to quantify browsing intensity (Adams 1959, de Vos 1964, Wolff 1978, Sinclair and Smith 1984, MacCracken et al.1988, Smith et al.1988). We chose to follow tracks to locate feeding sites to study winter hare diet within each cover type in our study area from January through March in 2000 through 2003 (Smith et al.1988). We chose this method because it was less expensive, less invasive to hares, coincided with other winter research efforts we were doing in the area, and because the low frequency of observing hares in our area made that method impractical.

Within a cover type we selected a fresh snowshoe hare track or trail and followed it until feeding sites were found. Since it was impossible to follow an individual hare we made a small loop through a particular cover type and followed any tracks that we crossed. We did not record a measure of effort spent searching each cover type for browsed plants. Although hares can feed on conifer needles without affecting stems, we counted only bites where stems were damaged by barking or clipping. Twigs browsed by hares were cut cleanly and at an angle, whereas bites by ungulates were more abrupt or torn (Telfer 1972). At each feeding site we recorded cover type, month, year, species of plant browsed, number of bites on each plant, plant height, and snow depth. Data were collected and summarized as percentages for the total diet over all years and for all years by cover type.

Results and Discussion

Vegetation Availability

Using circular plots randomly placed in each of eight cover types in the study area (Table 1) during summer months, we found that Lodgepole 3 stands had the highest density of trees > 0.1 m tall (average of

Table 1. Forested Cover Types in the Bear Creek Study Area.

Cover Type	Percent of Study Area	Description
Douglas fir	7.9	Old growth Douglas fir forest. Canopy is broken and the understory consists of some small to large spruce and fir.
Spruce Fir	15.9	Mature spruce fir forest. Stands dominated by Engelmann spruce and subalpine fir in both overstory and understory.
Mixed forest	8.4	Mature mixed forest, late succession to climax stage. Varied structure and age class representation with lodgepole pine, subalpine fir, Engelmann spruce, Douglas fir, and whitebark pine all in the overstory.
Lodgepole 0	14.8	Lodgepole pine 20-30 years post disturbance. Areas of regenerating seedlings and saplings before canopy closure created by logging between 1972 and 1977.
Lodgepole 1	15.6	Lodgepole pine 45-55 years post disturbance. Closed canopy of even-aged, usually dense, lodgepole pine. Stands were clear-cut between 1947 and 1952 and thinned in the mid 1970s.
Lodgepole 2	17.6	Lodgepole pine 100-300 years post disturbance. Closed canopy dominated by lodgepole pine. Understory of small lodgepole pine, whitebark pine, Engelmann spruce and subalpine fir seedlings.
Lodgepole 3	13.3	Lodgepole pine 300 plus years post disturbance. Broken canopy of mature lodgepole pine, but whitebark pine, spruce and subalpine fir also present. Understory of small to large spruce and fir saplings.
Sanitation Salvage	6.4	Sanitation salvages (mature forest partially harvested during 1986). Broken old growth canopy with a dense regenerating understory dominated by lodgepole pine.

18,382 trees/ha) followed by lodgepole 2 and mixed forest. Douglas fir stands had the lowest density with 1,263 trees/ha. As expected, lodgepole pine was the dominant tree species in the two youngest classes of lodgepole pine (Lodgepole 0 and Lodgepole 1), however, as the density of lodgepole pines decreased other coniferous species became more common in older lodgepole pine stands (Lodgepole 2 and 3).

Across all cover types, subalpine fir was the most abundant tree, comprising 55 percent of the total trees counted. Whitebark pine, lodgepole pine, Engelmann spruce, and Douglas fir comprised 21, 12, seven, and five percent of the total, respectively. Although subalpine fir and whitebark pine were the most common trees counted, many were <1 m tall, 89 and 92 percent, respectively, and were typically unavailable to snowshoe hares during late winter.

Lodgepole 0 stands had moderate-to-thick canopy near the ground, and the average tree height was 3 m. Lodgepole 1 stands ranged from 5 to 10 m tall but typically had lower branches within 2 m of the ground. The Lodgepole 2 type consisted of many small trees < 1 m tall and many mature trees with a canopy well above the ground thus providing very little food or cover for hares during winter. Dominant trees in Lodgepole 3 stands had a canopy well above the ground but understory trees and shrubs provided a thicker understory above 1 m than did Lodgepole 2 stands. Douglas fir forests had very little understory cover and a broken overstory well above the ground. Spruce-fir stands had dense overhead canopy that often hung within 2 m of the ground but typically had little or no understory growth more than 1 m tall. Mixed forests were structurally similar to Lodgepole 3 forests but typically had more species diversity, especially in the overstory.

Within 2.1-m radius circular plots divided into two height layers, we detected 15 species in layer 1 ($\leq$ 1 m of the ground) and 12 species in layer 2 (1-2 m above the ground). In layer 1, Lodgepole 0 contained the greatest number of species (13), followed by Lodgepole 1 and Sanitation Salvage with 12 each. Douglas fir stands contained the fewest with only seven detected species (Table 2).

In the second layer, Lodgepole 0, Lodgepole 1, Lodgepole 3, and Sanitation Salvage all had six species present while Lodgepole 2 and Spruce-fir only had three and two species, respectively (Table 2). Layer 1 contained both trees and shrubs. Subalpine fir and twinberry were

Table 2. Top three tree and shrub species present and percent canopy coverage for the two base layers (Layer 1 = 0-1 m, Layer 2 = 1-2 m) for each cover type.

Cover Type	No. of Species	Species 1	% Canopy	Species 2	% Canopy	Species 3	% Canopy
Layer 1							
Sanitation Salvage	12	Subalpine fir	13.3	Snowberry	7.0	Twinberry	3.8
Douglas fir	7	Snowberry	32.8	Common juniper	4.0	Spirea	2.9
Lodgepole 0	13	Lodgepole pine	18.4	Subalpine fir	7.2	Douglas fir	3.8
Lodgepole 1	12	Twinberry	5.5	Snowberry	2.9	Lodgepole pine	2.4
Lodgepole 2	10	Subalpine fir	5.8	Whitebark pine	3.5	Twinberry	1.8
Lodgepole 3	10	Subalpine fir	20.7	Twinberry	3.9	Whitebark pine	2.0
Spruce-Fir	10	Subalpine fir	11.5	Engelmann spruce	5.5	Twinberry	2.7
Mixed Forest	9	Subalpine fir	21.7	Engelmann spruce	6.3	Twinberry	5.7
Layer 2							
Sanitation Salvage	6	Engelmann spruce	6.3	Subalpine fir	5.9	Douglas fir	3.0
Douglas fir	5	Spirea	8.0	Whitebark pine	5.0	Douglas fir	1.1
Lodgepole 0	6	Lodgepole pine	14.0	Whitebark pine	12.2	Subalpine fir	7.0
Lodgepole 1	6	Lodgepole pine	6.1	Whitebark pine	4.5	Subalpine fir	4.0
Lodgepole 2	3	Whitebark pine	2.7	Lodgepole pine	2.0	Subalpine fir	2.0
Lodgepole 3	6	Subalpine fir	5.4	Engelmann spruce	5.0	Whitebark pine	1.2
Spruce-Fir	2	Subalpine fir	6.5	Engelmann spruce	5.8		
Mixed Forest	5	Subalpine fir	7.0	Whitebark pine	5.0	Engelmann spruce	4.3

common in Layer 1 among all cover types except Douglas fir. The second layer (1-2 m) contained mostly coniferous trees. Lodgepole pine was only common in the 1 to 2-m layer in Lodgepole 0, Lodgepole 1, and Lodgepole 2. Subalpine fir was common in all types except for Douglas fir, and whitebark pine was common in all types except Sanitation salvage and Spruce-fir. Douglas fir was only common in Layer 2 in Douglas fir and Sanitation salvage cover types.

Food Habits

While tracking snowshoe hares to locate feeding sites, we counted nearly 5000 bites and detected evidence of browsing on 18 different plant species. Lodgepole pine accounted for nearly 60 percent of bites, followed by Douglas fir and subalpine fir with 12 and 11 percent of total bites, respectively. Six plant species accounted for 1-4 percent of the hare diet; each of the remaining nine species accounted for < 1 percent of the total diet (Table 3). Hares typically clipped off the end of small branches or fed on needles and buds. Occasionally tips of branches were cut but left uneaten lying on top of the snow. Barking of stems by hares was very rare. Hares browsed predominately on coniferous trees (88 % of total diet), but also fed on several shrubs and forbs (12 %), the most common of which were juniper (*Juniperus communis*), annual composites (Compositeae), alder (*Alnus* sp.), and buffaloberry.

Snowshoe hare diet differed among cover types. Within Lodgepole 1 stands, 59 percent of the detected bites were on lodgepole pine, followed by Douglas fir and subalpine fir (Table 4). Lodgepole was the most browsed species in all cover types except for Douglas fir and Lodgepole 3. In Douglas fir stands, Douglas fir was browsed more than any other species and subalpine fir was browsed most often in Lodgepole 3 stands. When comparing percentage of browsing on lodgepole pine in the four successional stages, we detected decreased use from 92 percent in Lodgepole 0 stands to 27 percent in Lodgepole 3 stands.

The diet of snowshoe hares also differed among winter months. We recorded bites on 18 plant species during January but only nine in both February and March. Average snow depth across the study area increased over winter. January averaged 45.2 cm of snow while February and March averaged 69.6 cm and 95.7 cm, respectively.

Although we did not have direct information on plant availability where we collected dietary data, we assessed relative

Table 3. Plant species on which snowshoe hare browsing occurred and the percentage of the total number of bites recorded.

Scientific Name	Common Name	Percentage of Total Bites
Pinus contorta	Lodgepole pine	59.4
Pseudotsuga menziesii	Douglas fir	12.2
Abies lasiocarpa	Subalpine fir	11.3
Juniperus communis	Common juniper	3.7
Pinus albicaulis	Whitebark pine	3.2
Compositae	Annual composites	2.3
Alnus sp.	Alder	2.1
Picea engelmanii	Engelmann spruce	2.1
Shepherdia canadensis	Buffaloberry	1.0
Ribes sp.	Gooseberry	0.6
Salix sp.	Willow	0.6
Heracleum lanatum	Cow parsnip	0.5
Sambucus racemosa	Elderberry	0.4
Symphoricarpos albus	Snowberry	0.4
Lonicera involucrate	Twinberry	0.2
Vaccinium globulare	Huckleberry	0.2
Berberis repens	Oregon grape	0.0
Ceanothus velutinus	Evergreen ceanothus	0.0

Table 4 Comparison of the four most common species used in the hare diet with the availability of those species for each cover type. Availability is based on the percent canopy coverage from both layers combined from the 2.1 m radius vegetation plots.

Cover Type	Rs	*P*-Value	Species	Percent of Diet	Percent Canopy Coverage
Lodgepole 0	1.00	0.00	Lodgepole pine	92.3	29.5
			Subalpine fir	2.4	7.9
			Whitebark pine	1.9	5.6
			Ribes sp.	1.2	0.2
Lodgepole 1	0.40	0.60	Lodgepole pine	59.2	4.3
			Douglas fir	13.7	0.2
			Subalpine fir	12.0	2.4
			Common juniper	4.6	1.6
Lodgepole 2	-0.60	0.40	Lodgepole pine	43.3	0.6
			Douglas fir	32.6	0.5
			Whitebark pine	17.7	4.1
			Subalpine fir	5.7	3.8
Lodgepole 3	0.20	0.80	Subalpine fir	32.4	25.5
			Lodgepole pine	29.6	0.1
			Douglas fir	24.9	0.9
			Whitebark pine	10.4	1.6
Douglas fir	0.82	0.18	Douglas fir	92.0	0.7
			Subalpine fir	8.0	0.0
Mixed forest	-0.21	0.79	Lodgepole pine	46.8	0.0
			Subalpine fir	17.6	27.1
			Composites	10.1	0.0
			Common juniper	5.9	0.8
Spruce Fir	-0.80	0.20	Lodgepole pine	36.1	0.0
			Engelmann spruce	19.8	6.6
			Alder sp.	15.9	0.3
			Subalpine fir	11.1	11.7

availability and use by assuming that the combination of the two layers from the 2.1 m radius vegetation plots recorded during the summer was representative of plant availability during winter. We compared the percentage of diet for the four most commonly browsed species with an index of availability (percent canopy coverage) of those species for each cover type using a Spearman correlation matrix (Table 4). We found a positive correlation between diet and availability in the Lodgepole 0 cover type (Rs = 1.0, $P =$ 0.000) but no significant correlation between diet and plant availability in any other cover type.

Snowshoe hares fed on a variety of plant species and sizes. Plants from which we detected use by hares ranged in size from a few centimeters tall to 21 m tall, but 61 percent of the total bites were taken from plants less than 2 m tall. We commonly observed hares feeding on plants that were barely protruding above the snow, but they also fed on low branches of tall trees that drooped down to the snow level. These low branches provided 28 percent of the total bites.

We never observed hares digging in the snow to uncover food but found hares utilizing branches lying on the snow pack that had broken from the tops of mature trees or had been cut down by squirrels harvesting cones. Approximately 11 percent of the total bites we counted were on fallen branches. Hares fed on these branches in the same manner as a branch attached to a tree. Douglas fir and Lodgepole 2 stands had the highest percentage of their bites on fallen branches, both at nearly 80 percent. Lodgepole 3, mixed forest, and spruce-fir stands had between 20 and 30 percent of their bites on fallen branches. Lodgepole 0 and Lodgepole 1 had 0.5 and 5.7 percent of their bites taken from fallen branches, respectively. The majority of fallen branches eaten by hares were lodgepole pine, whitebark pine, and Douglas fir.

We observed hare browsing on a variety of plants (18 species), but the majority of browsing was on coniferous trees (88%) with lodgepole pine being utilized far more than any other species. Lodgepole pine was a common understory species in only three cover types. Whitebark pine was the fifth most commonly browsed species and was one of the three most abundant understory species in five cover types. Other studies have also reported snowshoe hares utilizing a wide variety of species during winter but also preferences for certain species (de Vos 1964, Wolff 1980, Hodges 2000). Although such preferences vary from place to place, winter hare diets typically consist of coniferous trees, shrubs, and some forbs (Wolff 1978). Where available, pine species are often a preferred winter browse for hares (de Vos 1964). When comparing the diets of hares within the four age classes of lodgepole pine stands, we detected substantially decreased use of lodgepole pine as stands matured. This is not surprising because our vegetation sampling suggested that density of lodgepole trees also declined as lodgepole forests matured.

Engelmann spruce was the eighth most common species in the hare diet (2% of total diet) even though it was common in the understory of four cover types. The majority of bites on spruce trees were taken from the upper branches of trees more than 5 m tall that were bent over under the weight of snow. Only a few bites were taken from spruce trees less than 2 m tall even though 1 to 2 m tall spruce trees were abundant in the study area. In some areas, especially in Canada where there is an absence of pines, spruce trees may be heavily utilized (Wolff 1978, Smith et al.1988). Smith et al. (1988) noticed hares avoiding juvenile spruce branches but found hares using mature side branches during periods of deep snow.

The amount of snowshoe hare browsing on subalpine fir and Douglas fir was very similar even though subalpine fir was much more common across the study area than was Douglas fir. In a study in Northwestern Montana, Adams (1959) found that hares fed heavily on Douglas fir during the winter; ponderosa pine (*Pinus ponderosa*) was moderately used. De Vos (1964) also found heavy browsing on pine species, while balsam fir (*Abies balsamea*) was used very little. Use of subalpine fir is seldom mentioned in literature on snowshoe hare diets.

Hares in our study consumed several species of shrubs and forbs (12% of total diet) including common juniper, annual composites, and alder. Several shrub species were relatively abundant, but all shrubs experienced low levels of use by hares. Due to accumulating snow, availability of these species was typically much lower compared to coniferous trees. Overall, number of species used declined as winter progressed, probably due to decreasing availability of many species as snow depths increased. Others have also noted use of shrubs and forbs by hares in winter (Smith et al.1988, Hodges 2000). Smith et al. (1988) observed hares browsing predominantly on deciduous shrubs, but their study area (Kluane, Yukon) had an abundance of shrub species while spruce was the only common conifer. Adams (1959) observed heavy utilization of Oregon grape (*Berberis repens)* in northwest Montana. We only noticed browsing on this species on one occasion, probably because it was buried under snow for most of the winter due to its short growth stature.

Hares typically feed by clipping the ends off of small twigs, but also may remove the bark of young trees (de Vos 1964). We observed barking on just a few occasions and only on small twigs of coniferous trees, never on trunks of trees or on deciduous shrubs. Barking can be detrimental to young stands of trees by girdling and killing them. Girdling often is associated with high hare density (de Vos 1964, Hodges 2000). We attribute infrequent barking in our study to a relatively low-to-moderate density of hares. Besides clipping small twigs, we observed that hares browsed on fallen branches lying on top of the snow pack (11% of total bites).

Use of fallen branches was most common in Lodgepole 2 and Douglas fir cover types. These types also had the lowest amount of available cover and browse within 5 m of the ground. Due to a lack of available browse growing in these stands, hares appeared to take advantage of this additional food source. Also, fallen branches may have made these less dense habitats tolerable to hares during winter. Use of fallen branches by hares had not been cited in other studies of snowshoe hare diet.

Conclusions

We found here, as reported for other areas, that snowshoe hares consumed a variety of plants during winter months but fed mostly on coniferous twigs that are available throughout winter, a period in which other plants were buried under snow. Lodgepole pine was an important diet item—common in regenerating lodgepole pine stands. The other two species most frequently consumed by hares, subalpine fir and Douglas fir, were most abundant in dense mature forest types. Mature forest stands and young regenerating stands are essential habitat types needed to ensure healthy populations of snowshoe hares in the northern portion of the GYE.

Acknowledgments

This project was funded by the USFS (Gallatin National Forest and Region 1) and the John and Kathryn Harris Foundation. Additional funding was provided to the Gardiner District research by G. Bennett, D. Ohman, and J. Wood. We wish to thank T. Hoffman for her help with statistics and GIS, E. Olexa for his assistance with statistics, and R. Burke for his help with logistics and climate information. R. Gowan, M. Cherry, M. Maj, and S. Kratville provided administrative and logistic support. Thanks are also due to the forest service volunteers who helped with data collection: M. Cobb, K. Gabrian, J. Hopkins, S. Coburn, K. Olson, M. Tyers, S. Yonge, N. Smith, K. Callard, and K. Gunter.

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Received 22 March 2008
Accepted 27 August 2008