The role of dietary fiber in dung size of bushy-tailed woodrats, *Neotoma cinerea*: its potential application to paleoclimatic interpretation

Jennifer C. Hallett  
*Desert Research Institute, Reno, Nevada*

Peter E. Wigand  
*Great Basin and Mohave Paleoenvironmental Consulting, Reno, Nevada*

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Woodrat dung collected from prehistoric woodrat middens fluctuates significantly in size. Incremental changes observed in average width of dung, from samples either within or between midden strata, appear to follow a pattern (Smith and Betancourt 1998). This pattern of change seems to mirror late Quaternary temperatures in the southwestern United States (Smith et al. 1995).

Since the 1960s, plant remains collected from prehistoric woodrat middens have been used as a source of proxy data to characterize prehistoric climates (Wells and Jorgensen 1964, Spaulding 1985, Mehringer and Wigand 1990, Thompson 1990, Wigand and Nowak 1992). Urine-encrusted strata from middens have been disaggregated to recover encased vegetation fragments that are then taxonomically identified and radiocarbon dated. Once these data are grouped with vegetational data collected from other analyzed midden strata, they are used to reconstruct past distributional ranges of plant species and changes in species distributions through time. Ultimately, using modern plant ecology, temporal and spatial distributional ranges of plant species are used to reconstruct prehistoric climate dynamics.

The study of prehistoric woodrat middens as climate change indicators has recently led to the use of woodrat dung as a potential research tool (Smith et al. 1995, Smith and Betancourt 1998). However, not all factors that affect dung size have been clearly elucidated. Therefore, its utility as an indicator of prehistoric climates remains unclear.

Dung-size variation may reflect changes in genotypic or phenotypic traits of the woodrat in response to environmental change. One of these traits, body size, would be expected to fluctuate over many generations. Two genetically similar rats might grow to different sizes depending upon food availability (Holter and Hayes 1977, Case 1978). Different body sizes may also reflect adult/juvenile and male/female differences in body size (e.g., male *Neotoma cinerea* may weigh up to 130 g more than females [Escherich 1981]). In using prehistoric dung samples to address body size, researchers have derived conclusions from dung measurement that may reflect shifts in gender of the woodrat occupying the nest, the presence of juvenile rats, and/or environmental factors.

Longer-term changes in body size may be the result of environmental conditions, such as

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**THE ROLE OF DIETARY FIBER IN DUNG SIZE OF BUSHY-TAILED WOODRATS, *NEOTOMA CINEREA*: ITS POTENTIAL APPLICATION TO PALEOCLIMATIC INTERPRETATION**

Jennifer C. Hallett1 and Peter E. Wigand2

**ABSTRACT.**—A laboratory study was conducted to examine causes underlying variation in woodrat dung size. Eight bushy-tailed woodrats, *Neotoma cinerea*, were captured and sequentially fed 2 diets of 46% and 63% neutral detergent fiber (NDF). Dung pellets were collected for 2 days following 7 days of acclimation to each diet. Length and width of oven-dried pellets ranged, respectively, from 8.3 to 10.2 mm and 3.2 to 4.9 mm for diet 1, and 8.9 to 12.4 mm and 3.6 to 4.7 mm for diet 2. Body weight ranged from 232.0 to 504.5 g and did not significantly affect dung size. A series of 2-factor analyses of variance with repeated measures and sequential Bonferroni tests was used to assess the effect of dietary fiber consumption on dung size. An increase in fiber intake led to a significant increase in dung length and dry dung weight but not dung width or body weight. Results suggest a relationship between dung length in prehistoric woodrat middens and changing climate, although the relationship is not clearly understood and needs further evaluation.

**Key words:** dung size variation, *Neotoma cinerea*, fiber consumption, body size, paleoclimate proxy data.

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1Desert Research Institute, 2215 Raggio Parkway, Reno, NV 89512.
2Great Basin and Mohave Paleoenvironmental Consulting, 2210 Seneca Drive, Reno, NV 89506.
temperature. A biogeographical hypothesis presented by Bergmann (1847) states that in colder climates populations of similar or the same animal species are larger bodied than in warmer climates. Changes in temperatures have been linked to altitudinal and latitudinal clinal trends in body size in many animal species (Boyce 1978, Burnett 1983, Benton and Uetz 1986, Bogdanowicz 1990). Perhaps the most important issue connected to body size change is how quickly it may occur.

Modern Neotoma spp. show substantial interspecific and intraspecific variation in body size (Hooper 1940, Hall 1946, Finley 1958, Brown 1968). Brown and Lee (1968) found body size of N. cinerea to be inversely correlated with temperature, concluding that populations followed Bergmann’s rule. Harris (1984) noted that structural traits in the teeth and jaw of prehistoric N. cinerea skeletal remains, collected from middens between 11,000 and 33,000 years old, show morphology similar to modern N. cinerea; however, he does not describe changes in body size.

Dung-size variation may also reflect woodrat diets. Woodrat dung is composed primarily of undigested food particles (structural carbohydrates) and metabolic products (bacteria and endogenous wastes; Van Soest 1982). Undigested food particles consist primarily of plant cell walls (cellulose, lignin, and hemicellulose), which make up most fiber components in the diet and cannot be broken down into nutrients (Van Soest 1982).

Since dung contains a large percentage of undigested fiber, the amount of fiber consumed in the diet and the ability to digest it should affect dung composition and, consequently, dung size. In one study Neotoma spp. dung contained 67% fiber produced on a 40% fiber diet (Justice and Smith 1992). The amount of fiber in forage relates to quality of the diet; high-fiber diets have lower nutritional value than low-fiber diets (Salisbury and Ross 1978, Van Soest 1982, Demment and Van Soest 1985). The ability to digest fiber varies; some herbivores can select diets higher in fiber than those with less efficient digestive systems (Demment and Van Soest 1985). Diet selection, though, is ultimately restricted by availability of forage.

In this study we assess the relationships among dietary fiber levels, body size, and dung size, and address the link between these factors and climate.

**Methods**

We trapped 8 adult bushy-tailed woodrats in the Granite Hills, approximately 25 km northwest of Reno, Nevada, between February and March 1993 and subjected them to a series of feeding trials analyzing the relationships among dung size, body size, and dietary fiber intake. The study animals were housed at the University of Nevada, Reno, Biology Department Animal Room and represented the range of adult body sizes typically recorded for the species. Variables selected to characterize body size were body length and body mass. These variables were selected based upon a correlation matrix comprising numerous body size variables measured after captivity. Strongly correlated variables were eliminated to reduce the number of variables in subsequent statistical analyses. We measured daily body weights for each diet. Mean body weight for each woodrat for each diet was used for statistical purposes.

Woodrats were housed for 1.5 to 2 months prior to feeding trials and were fed a diet of Purina rat chow and water from gravity-demand bottles. Woodrats were kept in individual cages with raised wire screens to avoid contact with fecal pellets. During feeding trials woodrats were provided, ad libitum, 2 natural-grain pelleted diets of differing levels of fiber. Diet 1 contained 14% acid detergent fiber (ADF), representing a higher-quality diet and, diet 2 contained 35% ADF. Feeding trials began after a 7-day acclimation period to diet 1 to completely void previously consumed food after Smith et al. (1995). Following acclimation each woodrat was given a preweighed daily portion of diet 1 for 2 days. All dung and orts (uneaten food particles) were collected every 24 hours. The same procedure was followed for diet 2.

To test for homogeneity in dung length and width variances, we performed a Hartley’s $F_{\text{max}}$ test for gender and diet combinations. A significant result would indicate that the data needed to be transformed. Following transformation (if necessary), diet effects were analyzed in a series of 2-factor (diet and gender) analyses of variance (ANOVA) with repeated measures on diet since individual woodrats
were observed under both diet conditions (PROC GLM; SAS Institute Inc. 1988). Mean dung widths and lengths were analyzed in separate ANOVAs. Carryover effects of ingesting the 2 diets in the same order were minimized by allowing sufficient time to elapse between the introduction of different diets so that the woodrats could acclimate. This reduced the need to randomize the sequence of feeding trials for each woodrat.

Three ANOVAs were also conducted to test for differences in average food intake, average number of fecal pellets excreted, and average dry weight of dung produced per day between the 2 diets. For all ANOVAs and regressions, we used a sequential Bonferroni test to control the probability of committing a type I error and to detect more than 1 false null hypothesis among tests.

Fiber assays were conducted on diets 1 and 2 at the Animal Nutrition Laboratory, University of Nevada, Reno. Neutral detergent fiber (NDF) analyses were conducted so other studies using NDF could be referenced. For statistical analysis fecal pellets representing each woodrat and diet were measured to assess the effects of fiber level intake on dung size. For those woodrats producing over 80 pellets per diet, we randomly selected a minimum of 80 dung pellets for measurement. The dung was oven-dried for 48 hours (to ensure that it was comparable to dung analyzed in prehistoric woodrat midden studies). Using digimatic calipers, we measured dung length and width and then calculated means representing each woodrat and diet. Relative precision for dung measurements was calculated (2% for dung width and 1% for dung length). Oven-dried dung was counted for each woodrat and diet and also weighed to assess differences in dung density between diets.

The relationship between body size and dung size was analyzed using simple linear regressions (PROC GLM; SAS Institute Inc. 1988). Eight linear regressions were conducted using dung length and width for each diet as individual dependent variables, and body length and weight as individual independent variables. Results from regressions dictated the type of statistical test to be conducted on diet effects. They determined the functional relationship between diet and dung length and width and whether or not dung length and width could be used as covariates. A non-significant result would eliminate the need to use body size variables (the continuous variables) in the statistical tests.

RESULTS

No statistically significant relationship could be detected between the independent variables, body length and body weight, and the dependent variables, dung width and dung length (Table 1). Only dung length data needed to be transformed, which was conducted by calculating the inverse of the mean dung length. For the ANOVA comparing diet 1 to diet 2, dung length for diet 2 was significantly longer ($F = 31.66, df = 1,6, P < 0.0013$). Remaining ANOVAs yielded nonsignificant results.

Woodrats consuming diet 2 produced a significantly heavier amount of dung than woodrats consuming diet 1 ($F = 8.19, df = 7, P < 0.002$); however, mean number of pellets produced per diet was not significantly different between experimental diets (Table 2). Mean amount of food (g) consumed per diet did not differ significantly between the 2 diets. NDF analyses resulted in 46% fiber for diet 1 and 63% fiber for diet 2 (ADF content for diet 1 was 14% and 35% for diet 2).

DISCUSSION

Dung length appeared to increase due to the greater amount of fiber in the dung during the feeding of diet 2. Lee (1992) indicates that as fiber consumption increases, more excreta (dry weight) is produced. Our study showed that total dry weight of dung produced per day for each diet significantly increased for the higher-fiber diet. Even though a weak relationship exists between mean number of pellets produced per day by each woodrat and the experimental diets, an increase in fiber intake leads predominantly to longer, or possibly denser, fecal pellets rather than an increase in number of pellets produced.

The direct physical influence of the digestive tract on fecal material might control dung length and width. Contractile waves in the colon form individual fecal pellets (Ruckebusch 1989); the material is forced out by lateral, outward compressions to create the length of fecal pellets. Larger amounts of material in the digestive tract from a higher-fiber diet might contribute to increased elongation of fecal pellets.
The amount of material in the digestive tract, and ultimately in the dung, is the result of fiber digestibility. Digestion of fiber varies due to several factors, including body size and passage rate through the gut (Demment and Van Soest 1985, Hammond and Wunder 1991, Justice and Smith 1992). In woodrats digestibility of fiber increases with increased body size (Justice and Smith 1992). Body size can also affect the amount of fiber consumed by a woodrat in its natural environment. Woodrats have been shown to select foods with greater nutritional content, which would lead to a rejection of foods with lower nutritive value such as those containing high fiber levels (Atsatt and Ingram 1983, Karasov 1989, Post 1993). For example, the smaller-bodied *N. lepida* selects foods with lower fiber content and as a result digests less fiber (Justice and Smith 1992).

Therefore, dung size variability would be expected to fluctuate within interspecific (and potentially intraspecific) natural woodrat populations because of the regulation of fiber selection and digestion primarily through body size differences. Our study did not indicate any effect of body size on dung width or length. This may be explained partially by the uniform fiber levels given woodrats in the experimental diets, disallowing them to select the amount of fiber. Regulation of fiber levels in our study combined with the digestive abilities of larger-bodied woodrats may have minimized any effect of body size on dung length and dung width. Variable digestive abilities might also make the relationship between fiber intake and dung size less obvious and may explain the nonsignificant finding for dung width and fiber intake.

Other studies have found that dung size varies directly with body size (Murie 1974, Luckenbach 1982, Smith et al. 1995). Smith et al. (1995) conducted a systematic evaluation of the relationship between dung size and body size. Their study analyzed only dung width and pellets wider than 4 mm for 3 woodrat species. In our experimental design we included the controlled testing of dietary fiber intake as well as body size on a single species to analyze causal relationships. Thus, although our study and that of Smith et al. (1995) are not directly comparable, results from each study illustrate a different general trend between dung width and body size. The different outcomes from the 2 studies emphasize the need for additional studies that combine elements from both experimental designs.

The significant relationship shown between dietary fiber and dung length is statistically more powerful when using a small number of woodrats. On the other hand, the lack of evidence of a relationship between body size and dung size might have been a function of the small number of experimental woodrats used in the study.

**Paleoecological Application of Woodrat Dung Size**

This study has documented that fiber intake affects dung length; however, a relationship between dung length and changing climate needs to be established. To quantify this relationship, the interactions between climatic variations and woodrat dung size are essential. A systematic approach to understanding how dung size changes in response to diet and body size can provide valuable insights into the functional ecology of woodrats and the broader implications for paleoenvironmental reconstruction.

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**Table 1. Differences in mean dung width and dung length between diets 1 and 2 produced by woodrats of distinct lengths and mean body masses.**

<table>
<thead>
<tr>
<th>Woodrat identification number</th>
<th>Mean body mass(^a) (g)</th>
<th>Body length (mm)</th>
<th>Mean dung width (mm)</th>
<th>Mean dung length (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Diet 1</td>
<td>Diet 2</td>
<td>Diet 1</td>
<td>Diet 2</td>
</tr>
<tr>
<td></td>
<td>Mean ( \pm ) s(_x)</td>
<td>Mean ( \pm ) s(_x)</td>
<td>Mean ( \pm ) s(_x)</td>
<td>Mean ( \pm ) s(_x)</td>
</tr>
<tr>
<td>8</td>
<td>440.0 ± 2.8</td>
<td>440.3 ± 0.5</td>
<td>18.8</td>
<td>3.35 ± 0.026</td>
</tr>
<tr>
<td>9</td>
<td>261.3 ± 1.3</td>
<td>232.0 ± 0.8</td>
<td>17.3</td>
<td>3.43 ± 0.025</td>
</tr>
<tr>
<td>10</td>
<td>327.6 ± 2.1</td>
<td>314.5 ± 6.5</td>
<td>19.7</td>
<td>3.28 ± 0.019</td>
</tr>
<tr>
<td>11</td>
<td>256.8 ± 1.6</td>
<td>255.7 ± 2.2</td>
<td>18.5</td>
<td>3.40 ± 0.054</td>
</tr>
<tr>
<td>13</td>
<td>295.3 ± 0.8</td>
<td>278.7 ± 3.2</td>
<td>17.8</td>
<td>3.22 ± 0.031</td>
</tr>
<tr>
<td>14</td>
<td>400.2 ± 3.5</td>
<td>396.7 ± 1.1</td>
<td>17.5</td>
<td>3.58 ± 0.032</td>
</tr>
<tr>
<td>15</td>
<td>504.5 ± 5.8</td>
<td>487.0 ± 3.9</td>
<td>18.0</td>
<td>4.87 ± 0.038</td>
</tr>
<tr>
<td>16</td>
<td>272.7 ± 3.5</td>
<td>295.2 ± 8.0</td>
<td>15.6</td>
<td>4.35 ± 0.026</td>
</tr>
<tr>
<td><strong>OVERALL</strong></td>
<td><strong>344.8 ± 89.7</strong></td>
<td><strong>337.5 ± 89.5</strong></td>
<td><strong>17.9</strong></td>
<td><strong>3.69 ± 0.026</strong></td>
</tr>
</tbody>
</table>

\( ^a \) Values represent mean \( \pm \) s\(_x\).
change, woodrat behavior, and plant community dynamics need to be studied in a modern setting. Such findings would be used to infer the amount and variation of fiber ingested in different plant communities (and nutrient availability) at various rainfall and temperature regimes observed in prehistory. Ultimately, dung-length measurements taken from ancient woodrat middens may be exploited as a proxy for climate change.

Fluctuation in fiber content is evident in individual plants due to seasonal influences and plant structure, and among and within vegetation communities (Demment and Van Soest 1985, Barboza and Hume 1992). These fluctuations, compounded with the ability of woodrats to select forage that meets nutritional requirements, imply that fiber intake varies significantly throughout the lifespan of a single woodrat and for populations living in different plant communities (Brown et al. 1972, Meserve 1974, Atsatt and Ingram 1983, Dial 1988, Justice and Smith 1992, Post 1993).

Dung-size variation from Neotoma cinerea in the Great Basin would be most indicative of climate change for several reasons. During the past 3200 years, populations of N. cinerea have not been particularly sensitive to habitat preferences, implying that they adapted (within the range of habitat preference) to different habitats, mesic and xeric, rather than shifting their distribution (Barnosky 1994, Hadly 1996). These variations reflect shifts between mesic and xeric species in the cold, wet late Pleistocene, 10,000–30,000 years BP, and between mesic and xeric species in the warm Holocene, since 10,000 BP. Resulting shifts in plant species along elevational and latitudinal gradients in response to changing climatic conditions must have influenced woodrat diet quality and resultant fiber intake.

Plant community changes in composition within the northwestern Great Basin have been documented since 30,000 years BP, including variations in numbers of herbaceous, shrubby, and arboreal species (Wigand and Nowak 1992, Nowak et al. 1994b). These variations reflect shifts between mesic and xeric species in the cold, wet late Pleistocene, 10,000–30,000 years BP, and between mesic and xeric species in the warm Holocene, since 10,000 BP. Resulting shifts in plant species along elevational and latitudinal gradients in response to changing climatic conditions must have influenced woodrat diet quality and resultant fiber intake.

The Great Basin has abundant woodrat nests that contain clearly distinguishable strata that can be sampled for woodrat dung and plant macrofossils ranging in age from modern to tens of thousands of years. Currently, data are being evaluated for dung width and length measurements from a single woodrat midden with multiple strata. This woodrat midden provides one of the best records of terrestrial history currently available for the northern Great Basin (Wigand and Nowak 1992, Nowak

<table>
<thead>
<tr>
<th>Woodrat identification number</th>
<th>Mean number of pellets produced per diet</th>
<th>Mean mass of food consumed per diet (g)</th>
<th>Mean mass of dung produced per diet (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Diet 1</td>
<td>Diet 2</td>
<td>Diet 1</td>
</tr>
<tr>
<td>8</td>
<td>107</td>
<td>118</td>
<td>14.4</td>
</tr>
<tr>
<td>9</td>
<td>66</td>
<td>78</td>
<td>8.2</td>
</tr>
<tr>
<td>10</td>
<td>86</td>
<td>103</td>
<td>8.3</td>
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<tr>
<td>11</td>
<td>51</td>
<td>61</td>
<td>10.2</td>
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<tr>
<td>13</td>
<td>101</td>
<td>125</td>
<td>15.5</td>
</tr>
<tr>
<td>14</td>
<td>79</td>
<td>109</td>
<td>21.6</td>
</tr>
<tr>
<td>15</td>
<td>63</td>
<td>126</td>
<td>18.7</td>
</tr>
<tr>
<td>16</td>
<td>63</td>
<td>69</td>
<td>10.8</td>
</tr>
<tr>
<td>Overall mean</td>
<td>77</td>
<td>99</td>
<td>13.5</td>
</tr>
</tbody>
</table>

*aUnable to measure
et al. 1994a, 1994b). Also, carbon isotopic analyses of plant materials from midden strata provide information regarding environmental stress, in particular drought- and cold-related water stress (Wigand et al. 1994). Additionally, measurements of juniper seed length provide a measure of effective moisture.

Smith et al. (1995) have implied that a relationship exists among woodrat body size, dung width, and climate change; this finding needs to be addressed when analyzing the relationships among fiber intake, dung length, and climate change. Since modern populations of woodrats show a tendency to follow Bergmann’s rule, it seems plausible that prehistoric populations of woodrats would respond similarly. In periods of drought or cold temperatures, as the woodrat’s body size increases, populations could be forced to consume higher-fiber forage. The cumulative effect of an increase in body size and fiber intake might potentially amplify dung size and be mistakenly attributed solely to body size. Body size and fiber intake may vary on different time scales. Fiber intake might influence dung-size variation more immediately and dramatically over the short term. Body size changes might occur more slowly and would be reflected in longer-term changes in dung size.

The purpose of this and similar studies is to understand how experimental findings relate to prehistoric woodrat response and climate change. A relationship between dung length and changing climate most likely exists; however, before dung length can be used to indicate paleoecological changes, underlying principles and interactions need to be clearly assessed.

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LITERATURE CITED


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