



Structural Density Assays of Leporid Skeletal Elements with Implications for Taphonomic, Actualistic and Archaeological Research

Barnet Pavao

Department of Anthropology, University of Georgia, Athens, GA 30602, U.S.A.

Peter W. Stahl

Department of Anthropology, Binghamton University, State University of New York, Binghamton, NY 13902–6000, U.S.A.

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Structural density assays of standardized bone scan sites are provided from six skeletons of four leporid taxa, including European or domestic rabbit (*Oryctolagus cuniculus*), Eastern cottontail (*Sylvilagus floridanus*), snowshoe hare (*Lepus canadensis*) and black-tailed jackrabbit (*Lepus californicus*). The results are discussed via comparison to published density figures for roughly similar-sized North American marmots (*Marmota* spp.). In the absence of reliable leporid density assays, archaeologists have substituted these figures as appropriate proxy measures. However, the data indicate important differences between leporid and marmot structural density assays, which can be considered as the expression of underlying anatomical dissimilarities. The implications of these results for assessing predator accumulation through application to published taphonomic and actualistic studies of leporid remains undertaken primarily in the Great Basin of the western United States, and for analyses of faunal assemblages in the American Southwest, are explored.

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Introduction

The structural properties of bone material are highly variable. Bone size, weight, density and overall morphology differ throughout the vertebrate skeleton in response to phylogeny, functional biomechanics and life history of the living organism. After death, these key variables are of fundamental importance to all aspects of assemblage formation as they influence subsequent preservation of the organism's remains in the buried record. In particular, structural density appears to be a crucial property affecting the character of deposited bone assemblages, and was accordingly investigated in a number of pioneering studies (e.g., Brain, 1967, 1969; Voorhies, 1969; Behrensmeyer, 1975; Binford & Bertram, 1977). Lyman (1982, 1984; and see, 1994, chapter 7) established the baseline for our current understanding of this highly variable property through his innovative use of photon absorptiometry. Not only did his study offer reliable and replicable density values for New World deer (*Odocoileus* spp.), domestic sheep

(*Ovis aries*) and pronghorn antelope (*Antilocapra americana*), it presented the data in a way that could be readily incorporated into the analysis of fragmented assemblages.

Almost immediately these measures of artiodactyl bone density were applied to critical assessments of Binford's (1978) models for understanding the variable accumulation of bone assemblages. Binford's models were ethnographically and experimentally grounded in a knowledge of how human consumptive strategies could be related to the economic anatomy of prey taxa. However, the structural density studies convincingly demonstrated the potentially equifinal nature of inferences based upon utility curves that did not take into account ultimate causation by structural bone density (Lyman, 1985, 1991, 1992, 1993, 1994; Grayson, 1988, 1989). In addition, other studies explored different ways in which structural density assays could ultimately increase the resolution of archaeological inferences based on numerical compositions and/or spatial arrangements of analysed skeletal part representation (e.g., Klein, 1989; Lyman, 1988; Stahl & Zeidler,

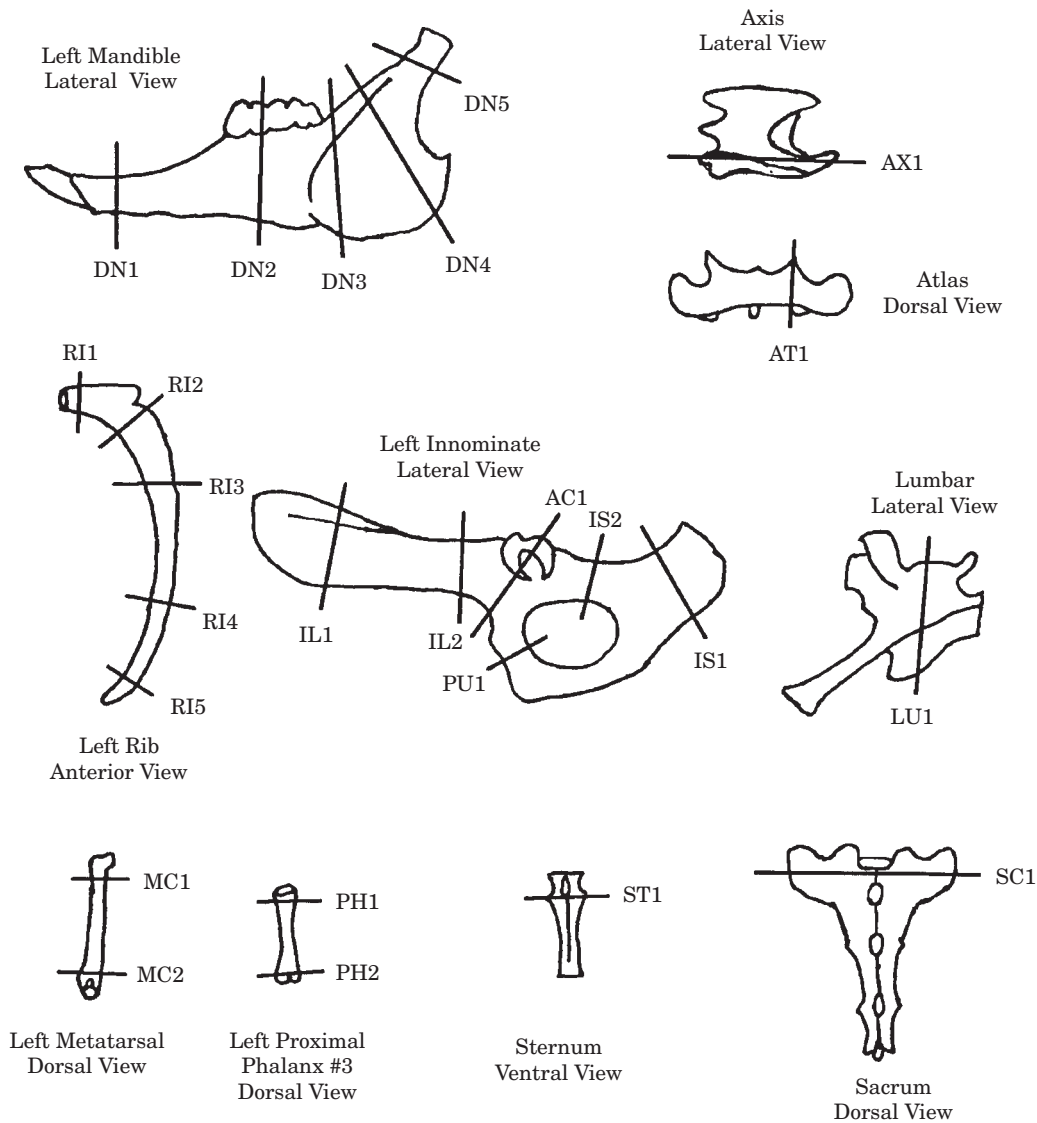


Figure 1. Scan sites.

1988, 1990; Grayson, 1989; Marean & Spencer, 1991; Marshall & Pilgrim, 1991; Blumenschine & Marean, 1993; Morlan, 1994; Schmitt & Juell, 1994; Schmitt & Lupo, 1995; Stahl, 1995; Marean & Frey, 1997; Quirt-Booth & Cruz-Urbe, 1997; Cruz-Urbe & Klein, 1998; Diab, 1998).

A common and potentially problematic obstacle to the successful application of structural density assays is the restricted range of measured taxa. Out of necessity, many studies applied assays of one taxon (especially *Odocoileus* spp.) to dissimilar taxa for which comparable data were unavailable, under the assumption that they might serve as adequate or appropriate proxy measures. Explorations into the subtleties of variable density between comparable bone sites across taxa have revealed that these assumptions may often be incorrect (e.g., Kreutzer, 1992; Lyman, Houghton &

Chambers, 1992). Kreutzer (1992: 291) states that “where great differences in body size and behavioral adaptation exist between the model and subject taxa, the model may be entirely inappropriate or, at best, provide only a blunt instrument capable of detecting gross patterning across the assemblage”.

Clearly, it is important to establish a comprehensive catalogue of standardized measures across skeletons from different taxa. Since Lyman’s pioneering study of selected artiodactyls, many researchers have successfully applied photon absorptiometry to provide reliable structural density assays for bison (*Bison bison*), marmots (*Marmota* spp.), New World camelids (*Lama* spp.), phocid seals (*Phoca* spp.), chinook salmon (*Oncorhynchus tshawytscha*) and humans (*Homo sapiens*) (Elkin & Zanchetta, 1991; Chambers, 1992; Kreutzer, 1992; Lyman Houghton & Chambers, 1992;

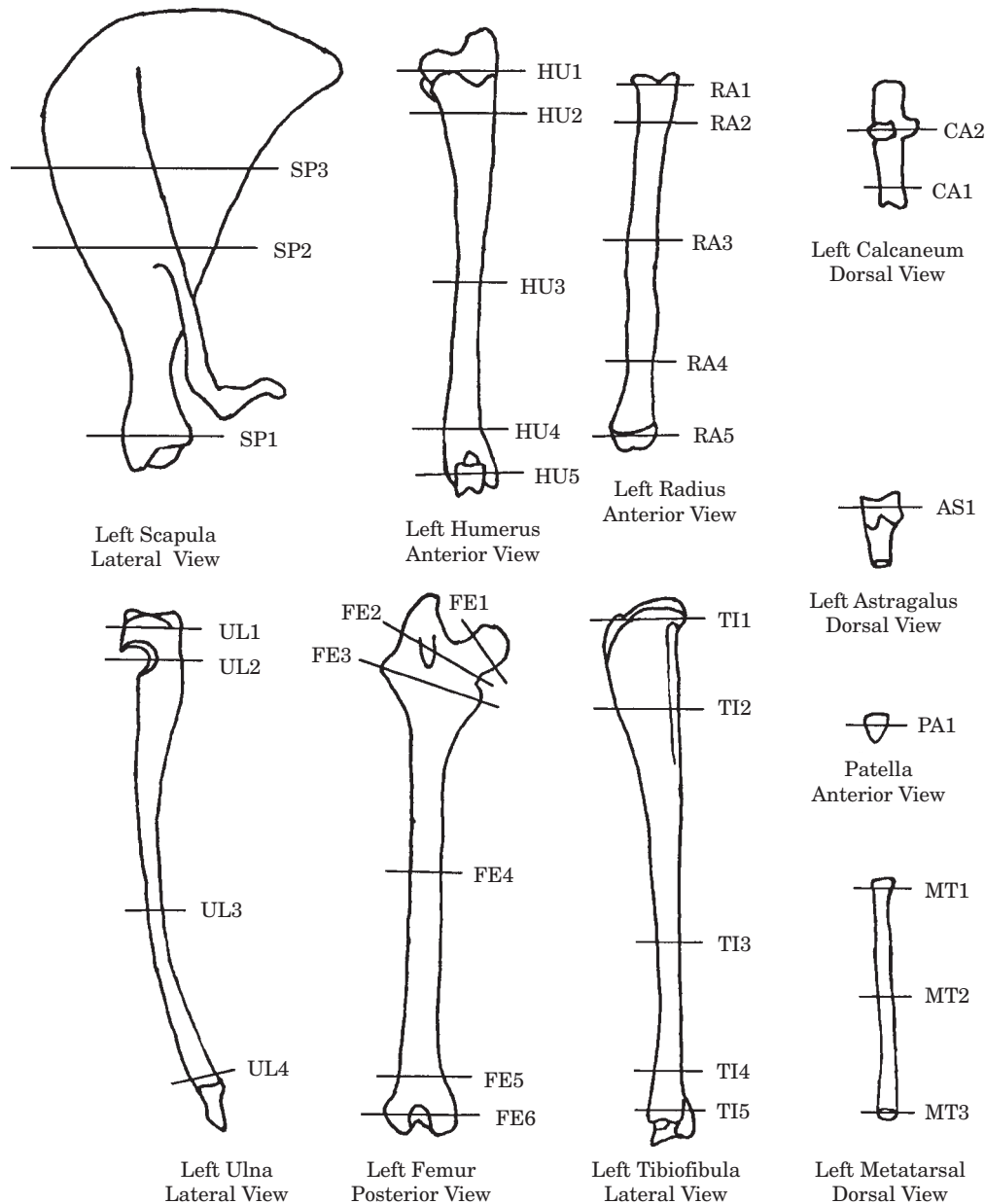


Figure 2. Scan sites.

Lyman, 1994: chapter 7; Butler & Chatters, 1994; Elkin, 1995; Galloway, Willey & Snyder, 1997). Despite this encouraging increase in the number and variety of studied taxa, many more studies are needed. To date, no comparable structural density measures are available for leporid (rabbits and hares) skeletons, despite their global and temporal importance in archaeological and palaeontological assemblages.

In this paper, we present structural density assays of standardized bone scan sites from the skeletons of four leporid taxa: European or domestic rabbit (*Oryctolagus cuniculus*), Eastern cottontail (*Sylvilagus floridanus*), snowshoe hare (*Lepus canadensis*) and black-tailed jackrabbit (*Lepus californicus*). First, the

materials and methods used to derive the structural density assays are outlined. Next, we discuss our results via comparison to published density figures for North American marmots. The implications of these leporid structural density assays for assessing predator accumulations are explored through application to published taphonomic and actualistic studies of leporid remains undertaken primarily in the Great Basin of the western United States. Their implications for zooarchaeological interpretation are then explored through application to a published faunal assemblage from the American Southwest. This is followed by a brief concluding statement with some further suggestions.

Table 1. Volume density assays of selected scan sites (g/cm^3)

Scan site		<i>O. cuniculus</i>	<i>S. floridanus</i>	<i>L. canadensis</i>	<i>L. californicus</i>	Leporid mean	Rank
AC1	VD _{SA}	0.42	0.39	0.43	0.32	0.39	6
	VD _{LD/BT}	0.08	0.08	0.08	0.05	0.07	26
AS1	VD _{SA}	0.28	0.26	0.23	0.19	0.24	30
	VD _{LD/BT}	0.1	0.08	0.06	0.05	0.07	30
AT1	VD _{SA}	0.33	0.11	0.24	0.14	0.21	31
	VD _{LD/BT}	0.07	0.02	0.05	0.03	0.04	50
AX1	VD _{SA}	0.46*	0.36	0.32	0.27	0.35	12
	VD _{LD/BT}	0.55*	0.06	0.13	0.05	0.2	3
CA1	VD _{SA}	0.2	0.27	0.3	0.26	0.26	27
	VD _{LD/BT}	0.09*	0.12	0.12	0.11	0.11	8
CA2	VD _{SA}	0.34	0.35	0.4	0.43	0.38	8
	VD _{LD/BT}	0.08	ND	ND	ND	0.08	19
DN1	VD _{SA}	0.43	0.37	0.51	0.22	0.38	7
	VD _{LD/BT}	0.19	0.18	0.2	0.09	0.16	4
DN2	VD _{SA}	0.74	0.58	0.7	0.38	0.6	1
	VD _{LD/BT}	0.22	0.24	0.24	0.15	0.22	2
DN3	VD _{SA}	0.28	0.36	0.3	0.13	0.27	24
	VD _{LD/BT}	0.07*	ND	ND	ND	0.07	27
DN4	VD _{SA}	0.22	0.06	0.21	0.08	0.14	37
	VD _{LD/BT}	0.07*	ND	ND	ND	0.07	33
DN5	VD _{SA}	0.14	0.03	0.12	0.08	0.09	48
	VD _{LD/BT}	0.12	0.03	0.08	0.07	0.07	25
FE1	VD _{SA}	0.26	0.31	0.28	0.27	0.28	19
	VD _{LD/BT}	0.08	0.1	0.07	0.08	0.08	18
FE2	VD _{SA}	0.28	0.29	0.3	0.23	0.28	20
	VD _{LD/BT}	0.07	0.08	0.08	0.06	0.07	29
FE3	VD _{SA}	0.41	0.42	0.3	0.33	0.37	10
	VD _{LD/BT}	0.09	0.13	0.78	0.09	0.27	1
FE4	VD _{SA}	0.39	0.34	0.25	0.33	0.33	14
	VD _{LD/BT}	0.13	0.14	0.07	0.11	0.11	9
FE5	VD _{SA}	0.26	0.33	0.28	0.26	0.28	21
	VD _{LD/BT}	0.06*	0.08*	0.07	ND	0.07	34
FE6	VD _{SA}	0.63	0.54	0.59	0.54	0.58	2
	VD _{LD/BT}	0.09*	0.08*	ND	ND	0.09	17
HU1	VD _{SA}	0.43	0.46	0.49	0.45	0.46	4
	VD _{LD/BT}	0.06	0.07	0.07	0.06	0.07	38
HU2	VD _{SA}	0.25	0.3	0.28	0.22	0.26	28
	VD _{LD/BT}	0.05	0.1	0.07	0.05	0.07	35
HU3	VD _{SA}	0.34	0.23	0.24	0.17	0.25	29
	VD _{LD/BT}	0.13	0.12	0.08	0.07	0.1	13
HU4	VD _{SA}	0.4	0.26	0.23	0.2	0.27	23
	VD _{LD/BT}	0.15	0.13	0.09	0.09	0.11	7
HU5	VD _{SA}	0.4	0.37	0.37	0.32	0.37	9
	VD _{LD/BT}	0.11	0.11	0.1	0.09	0.1	10
IL1	VD _{SA}	0.38	0.28	0.26	0.21	0.28	22
	VD _{LD/BT}	0.21	0.15	0.06	0.04	0.11	6
IL2	VD _{SA}	0.45	0.35	0.29	0.32	0.35	13
	VD _{LD/BT}	0.14	0.15	0.09	0.12	0.12	5
IS1	VD _{SA}	0.17	0.24	0.16	0.14	0.18	32
	VD _{LD/BT}	0.06	0.12	0.06	0.06	0.07	24
IS2	VD _{SA}	0.37	0.27	0.28	0.32	0.31	16
	VD _{LD/BT}	0.12	0.09	0.07	0.11	0.1	11
LU1	VD _{SA}	0.35	0.35	0.31	0.18	0.3	17
	VD _{LD/BT}	0.06	0.06	0.05	0.03	0.05	46
MC1	VD _{SA}	0.12	0.05*	0.07	0.11	0.09	47
	VD _{LD/BT}	0.06	0.05*	0.06	0.06	0.06	43
MC2	VD _{SA}	0.13	0.07	0.09	0.13	0.11	42
	VD _{LD/BT}	0.1	0.05	0.05	0.08	0.07	28
MT1	VD _{SA}	0.11*	0.1*	0.17	0.13	0.13	39
	VD _{LD/BT}	0.03*	0.04*	0.05	0.06	0.04	47
MT2	VD _{SA}	0.06*	0.06*	0.1	0.1	0.08	49
	VD _{LD/BT}	0.04*	0.05*	0.07	0.07	0.06	42
MT3	VD _{SA}	0.12*	0.11	0.15	0.09	0.12	40
	VD _{LD/BT}	0.07	0.06	0.07	0.03	0.06	41
PA1	VD _{SA}	0.25*	0.07*	0.04	0.07	0.11	43
	VD _{LD/BT}	0.14*	0.04*	0.04	0.04	0.07	37
PH1	VD _{SA}	0.1	0.02*	0.05	0.04	0.05	55
	VD _{LD/BT}	0.07	0.01*	0.05	0.03	0.04	51
PH2	VD _{SA}	0.08	0.01*	0.03	0.01	0.03	59
	VD _{LD/BT}	0.07	0.01*	0.02	0.01	0.03	55
PU1	VD _{SA}	0.17	0.04	0.08	0.09	0.1	46
	VD _{LD/BT}	0.07	0.02	0.04	0.04	0.04	48

Table 1. Continued

Scan site		<i>O. cuniculus</i>	<i>S. floridanus</i>	<i>L. canadensis</i>	<i>L. californicus</i>	Leporid mean	Rank
RA1	VD _{SA}	0.14*	0.11*	0.2	0.18	0.16	35
	VD _{LD/BT}	0.04*	0.06*	0.1	0.06	0.07	36
RA2	VD _{SA}	0.14*	0.07*	0.11	0.12	0.11	44
	VD _{LD/BT}	0.06*	0.05*	0.06	0.06	0.06	40
RA3	VD _{SA}	0.13*	0.07*	0.13	0.15	0.12	41
	VD _{LD/BT}	0.09*	0.06*	0.08	0.1	0.08	21
RA4	VD _{SA}	0.12*	0.09*	0.09	0.21	0.13	38
	VD _{LD/BT}	0.05*	0.05*	0.04	0.1	0.06	39
RA5	VD _{SA}	0.11*	0.08*	0.12	0.28	0.15	36
	VD _{LD/BT}	0.04*	0.04*	0.06	0.07	0.05	44
RI1	VD _{SA}	0.04	0.04	0.03	0.05	0.04	57
	VD _{LD/BT}	0.04	0.05	0.04	0.06	0.05	45
RI2	VD _{SA}	0.06	0.08	0.06	0.07	0.07	50
	VD _{LD/BT}	0.04	0.05	0.05	0.04	0.04	49
RI3	VD _{SA}	0.07	0.04	0.01	0.04	0.04	58
	VD _{LD/BT}	0.04	0.03	0.01	0.02	0.02	56
RI4	VD _{SA}	0.05	0.04	0.05	0.01	0.04	56
	VD _{LD/BT}	0.08	0.03	0.04	0.01	0.04	52
RI5	VD _{SA}	0.01	0.01	0.03	0.01	0.02	60
	VD _{LD/BT}	0.01	0.02	0.04	0.01	0.02	58
SC1	VD _{SA}	0.43	0.42	0.36	0.23	0.36	11
	VD _{LD/BT}	0.09	0.12	0.07	0.04	0.08	20
SP1	VD _{SA}	0.33	0.28	0.23	0.24	0.27	26
	VD _{LD/BT}	0.07	0.08	0.06	0.15	0.09	14
SP2	VD _{SA}	0.13	0.07	0.12	0.07	0.1	45
	VD _{LD/BT}	ND	ND	ND	ND	ND	ND
SP3	VD _{SA}	0.09	0.04	0.07	0.05	0.07	51
	VD _{LD/BT}	ND	ND	ND	ND	ND	ND
ST1	VD _{SA}	0.07	0.05*	ND	0.05	0.06	53
	VD _{LD/BT}	0.03	0.02*	ND	0.01	0.02	57
TI1	VD _{SA}	0.54	0.6	0.63	0.45	0.56	3
	VD _{LD/BT}	0.09	0.08	0.08	0.06	0.08	23
TI2	VD _{SA}	0.33	0.33	0.32	0.28	0.32	15
	VD _{LD/BT}	0.09	0.1	0.08	0.09	0.09	16
TI3	VD _{SA}	0.3	0.33	0.25	0.31	0.3	18
	VD _{LD/BT}	0.1	0.12	0.08	0.1	0.1	12
TI4	VD _{SA}	0.26	0.28	0.21	0.31	0.27	25
	VD _{LD/BT}	0.06	0.08	0.05	0.09	0.07	31
TI5	VD _{SA}	0.44	0.42	0.43	0.43	0.43	5
	VD _{LD/BT}	0.06	0.08	0.07	0.06	0.07	32
UL1	VD _{SA}	0.2	0.16	0.13	0.16	0.16	34
	VD _{LD/BT}	0.09	0.08	0.06	0.08	0.08	22
UL2	VD _{SA}	0.23	0.19	0.14	0.14	0.18	33
	VD _{LD/BT}	0.12	0.12	0.06	0.07	0.09	15
UL3	VD _{SA}	0.12*	0.11*	0.02	0.001	0.06	52
	VD _{LD/BT}	0.03*	0.07*	0.01	0.00	0.03	56
UL4	VD _{SA}	0.14*	0.06*	0.06	0.001	0.06	54
	VD _{LD/BT}	0.06*	0.04	0.04	0.00	0.04	53

Density values (VD_{SA}=Shape-Adjusted Volume Density, VD_{LD/BT}=Volume Density derived by dividing LD {BMD} by BT) listed for *O. cuniculus* and *S. floridanus* are averaged values from two individual skeletons for each taxon, except where unavailable and noted by an asterisk. For purpose of presentation, most values are rounded to two decimal places; however, exact values were used in all computations. Rank values are listed for the averaged value of each leporid scan site.

Materials and Methods

Six complete leporid skeletons from comparative collections in the Departments of Anthropology and Biology at Binghamton University were used in the study. Two adult specimens each of *Sylvilagus floridanus* and *Oryctolagus cuniculus* along with one adult *Lepus canadensis* and one immature *L. californicus* were chosen. The studied sample is admittedly small; however, it allows us to tentatively explore variation in bone density at the generic, inter-, and intra-specific levels. The skeletally immature specimen

may also provide a provisional impression of how individual ontogeny affects bone density, at least for this and related taxa.

For consistency, we followed, wherever feasible, the methods published by Lyman (1984) and Kreutzer (1992). The scan sites chosen for investigation correspond as closely as possible to those used in Lyman, Houghton & Chambers' (1992) study of *Marmota* spp. skeletons. Certain sites found on the marmot, and not on the leporid skeleton (e.g., separate fibula, clavicle), were obviously eliminated. Other sites potentially useful for resolving aspects of locomotion

(e.g., including the metacarpus in addition to the metatarsus) were added. Wherever appropriate, the left side of the skeleton was measured unless it was unavailable, in which case its right counterpart was substituted. Certain scan sites on some skeletons were not available for study, and these are noted. The scan sites and abbreviations used are illustrated in Figures 1 and 2.

Bone mineral density was measured using the Spine Scan Analysis function of a Lunar Radiation Corporation DP3 Dual-photon Absorptiometer with attached version 1.2 analytical software. The analysis allows clinical measurement of Bone Mineral Content (BMC, in g/cm) and computes Bone Mineral Density (BMD), also referred to as Linear Density (LD, in g/cm²), for defined regions of interest in the human lumbar region. In this study we chose the smallest possible region of interest, employing a scan length of 2 mm. Each bone was scanned in the same orientation on a 1 mm thick aluminum sheet which was used to mimic soft tissue (e.g., Kreutzer, 1992: 275). The aluminum was separately scanned prior to the study in order to measure background extraneous mineral density. The readings obtained for the aluminum sheet ranged from 0.00 to 0.03 g/cm².

Inevitable problems encountered in measuring bones of this small size necessitated certain on-screen data manipulations. As the machine measures the average bone mineral content across the scan site, it is important to ensure that only the defined portion of the bone element is measured. Normally, the contours of the bone element are highlighted on-screen as the machine automatically detects the outside edges of high density bone. Often, however, the small size and/or limited amount of measurable bone mineral in some elements causes the machine to define its region of analytical interest in a straight line from one area of high density to the next. This results in the inclusion of air space which would, if not eliminated, erroneously skew the averaged measure across the scan. In these cases, we had to manually outline the element on-screen in order to ensure that the defined analytical region of interest (BW, or Bone Width) corresponded with the contours of the skeletal element as closely as possible.

The machine automatically calculated BMD (g/cm²). Previous studies derived Volume Density (VD, in g/cm³), from LD divided by the estimated area of each site. LD was estimated by dividing BW into BMC (Lyman, 1984:273). For comparability, we derived BMC (g/cm) through multiplying the BMD (g/cm²) reading by area (cm²), expressed as BW multiplied by the standardized region of interest (2 mm). BMC for each scan site was then divided by its respective volume, expressed as area multiplied by maximum bone width (BT). Our areal estimations differ from previous studies. The small size of many scan sites constrained us from using Kreutzer's (1992) method for area determination. We also chose not to follow the alternative method which uses BT to norm all the

results to a square or rectangle (Lyman, 1984), as this procedure would have further underestimated the already low bone mineral values. Instead, we computed area by assigning each scan site a geometric shape (e.g., circle, rectangle, trapezoid, triangle) that most closely approximated its profile. We refer to these measurements as "shape-adjusted" (VD_{SA}=Shape-Adjusted Volume Density). In order to facilitate comparison with results from previous studies, we present a second set of calculations in which areas are normed to a square or rectangular shape, through dividing BMD by BT ($VD_{LD/BT}$ =Volume Density, or LD {BMD} ÷ BT). All measurements were made with a sliding digital caliper. The effect of different area computations on final results are explored below. We are currently investigating the use of digital imaging and computer-aided measurement of cross-sectional area, and expect to publish these findings in a separate article. Nevertheless, disparity in areal computation should be taken into consideration whenever comparing data between different studies.

Results and Discussion

The Volume Density (VD) assays of 60 selected scan sites from six skeletons representing the four leporid taxa are presented in Table 1. A fifth column in the table displays averaged measures for all leporid taxa combined, and a sixth displays accompanying rank orders for each mean value. Values for both methods of cross-sectional area computation (VD_{SA} and $VD_{LD/BT}$) are presented. The data should be viewed as provisional, due to the small number of skeletons examined and the potentially great range of individual variation within each taxon. For example, although significant and positively correlated, the two specimens of *O. cuniculus* have lower Pearson's *r* values ($r=0.763$, $P<0.001$) than similar intra-familial comparisons. This small sample suggests the possibility that intra-specific variation can be greater than inter-specific variation, particularly as they are domesticated animals which could exhibit potentially extreme variation. It is, however, important to note that all combinations of comparisons between the separate taxa are both significantly and positively correlated (Table 2, and compare with Table 3 which lists correlations computing $VD_{LD/BT}$). Although each correlation is high, it is not surprising that the lowest correlation values involve comparisons between *L. californicus* and all three remaining taxa. The *L. californicus* specimen is obviously immature, and a perusal of Table 1 shows that much of this difference is a factor of lower VD assays of scan sites concentrated throughout the mandible, as well as the slender and unfused distal portions of the ulna.

The data appear to suggest some major differences between the structural density of leporid skeletal elements and those of marmots (Lyman, Houghton &

Table 2. Correlation of volume density assays (VD_{SA} =Shape-Adjusted Volume Density) between four leporid and two *Marmota* taxa

	<i>O. cuniculus</i>	<i>S. floridanus</i>	<i>L. canadensis</i>	<i>L. californicus</i>	<i>M. flaviventris</i>	<i>M. monax</i>
<i>O. cuniculus</i>	*	0.9162 (60)	0.9116 (59)	0.8192 (60)	-0.3707 (51) $P=0.0074$	-0.1987 (57) $P=0.1385$
<i>S. floridanus</i>	0.9162 (60)	*	0.9329 (59)	0.8751 (60)	-0.5134 (51)	-0.3064 (57) $P=0.0205$
<i>L. canadensis</i>	0.9116 (59)	0.9329 (59)	*	0.8559 (59)	-0.4275 (51) $P=0.0018$	-0.3455 (56) $P=0.0091$
<i>L. californicus</i>	0.8192 (60)	0.8751 (60)	0.8559 (60)	*	-0.4331 (51) $P=0.0015$	-0.1271 (57) $P=0.3461$
<i>M. flaviventris</i>	-0.3707 (51) $P=0.0074$	-0.5134 (51)	-0.4275 (51) $P=0.0018$	-0.4331 (51) $P=0.0015$	*	0.7526 (54)
<i>M. monax</i>	-0.1987 (57) $P=0.1385$	-0.3064 (57) $P=0.0205$	-0.3455 (56) $P=0.0091$	-0.1271 (59) $P=0.3461$	0.7526 (54)	*

Pearson r values with sample sizes shown in parentheses, all $P<0.001$ except where otherwise indicated.
Marmota data from Lyman, Houghton & Chambers (1992).

Table 3. Correlation of volume density assays ($VD_{LD/BT}$ =Volume Density derived by dividing LD {BMD} by BT) between four leporid and two *Marmota* taxa

	<i>O. cuniculus</i>	<i>S. floridanus</i>	<i>L. canadensis</i>	<i>L. californicus</i>	<i>M. flaviventris</i>	<i>M. monax</i>
<i>O. cuniculus</i>	*	0.3781 (55) $P=0.0044$	0.1984 (53) $P=0.1545$	0.2234 (53) $P=0.1078$	-0.0946 (51) $P=0.5088$	-0.0483 (55) $P=0.7263$
<i>S. floridanus</i>	0.3781 (55) $P=0.0044$	*	0.4059 (53) $P=0.0026$	0.6371 (53)	-0.1642 (49) $P=0.2597$	-0.1006 (52) $P=0.4778$
<i>L. canadensis</i>	0.1984 (53) $P=0.1545$	0.4059 (53) $P=0.0026$	*	0.2945 (52) $P=0.0340$	-0.1094 (48) $P=0.4592$	-0.0166 (50) $P=0.9088$
<i>L. californicus</i>	0.2234 (53) $P=0.1078$	0.6371 (53)	0.2945 (52) $P=0.0340$	*	-0.0259 (47) $P=0.8627$	0.1715 (50) $P=0.2338$
<i>M. flaviventris</i>	-0.0946 (51) $P=0.5088$	-0.1642 (49) $P=0.2597$	-0.1094 (48) $P=0.4592$	-0.0259 (47) $P=0.8627$	*	0.7526 (54)
<i>M. monax</i>	-0.0483 (55) $P=0.7263$	-0.1006 (52) $P=0.4778$	-0.0166 (50) $P=0.9088$	0.1715 (50) $P=0.2338$	0.7526 (54)	*

Pearson r values with sample sizes shown in parentheses, all $P<0.001$ except where otherwise indicated.
Marmota data from Lyman, Houghton & Chambers (1992).

Chambers, 1992), the only other comparably-sized mammalian taxa for which data are available. This is clearly illustrated in Table 2. Intra-familial, leporid and marmot density assays are strongly and positively correlated; however, inter-familial comparisons reveal relatively weak and negative correlations in all conceivable permutations. This general pattern also appears to be consistent for correlations based on different areal computations (Table 3). Throughout the skeleton, marmot VD assays are generally greater than their leporid counterparts. We believe that these differences reflect structural differences between very dissimilar taxa; however, we first explore the possibility that the discrepancies may be attributed to differing techniques of volume estimation.

We estimated the shape-adjusted volume (VD_{SA}) of each scan site by first assigning each a closely approximated geometric shape (i.e., circle, rectangle, trapezoid, triangle), and then multiplying BT by BW by 2 mm. We prefer this alternative to norming the area estimate to a square or rectangular shape by dividing an averaged BT into each LD (e.g., Lyman, Houghton & Chambers, 1992: 562) for primarily two reasons. First, square or rectangular shape estimates

necessarily incorporate a certain amount of air space which could systematically underestimate the derived VD values, not counting internal pore space (Lyman, 1984: figure 3). Many of the leporid density values are already quite low and we considered it important to factor out as much imprecision as possible. Second, the use of square and rectangular shape estimates strongly reduces the degree of variability in scan cross-sectional shape. This is particularly important for many of the small scan sites throughout the leporid skeleton, which become conflated into homogenous VD values (Table 1), leaving little or no margin for error. Although our use of various geometric shapes was prompted by an attempt to mitigate some of the potential artificial uniformity in cross-sectional shape estimation, it certainly introduces its own potential bias.

Can the observed differences between leporids and marmots be attributed to contrasting methods of volume estimation rather than variation in structural density? Correlations between shaped-adjusted (VD_{SA}) estimates and the marmot data tend to be weakly negative in all possible permutations (Table 2). A comparison of leporid $VD_{LD/BT}$ estimates with marmot

Table 4. Correlation of averaged volume density assays (VD_{SA} = Shape-Adjusted Volume Density) with *Sylvilagus* and *Lepus* bone survivorship at five accumulation sites (from Hockett, 1993: chapter 6)

	Two Ledges Chamber (Owl/Woodrat/Carnivore)	Matrac Roost (Golden Eagle)	Waterfall Roost (Prairie Falcon)	Little Brown Bat Fissure (Woodrat/Raptor/Bobcat/ Coyote/Fox)	64 Woodrat Nests (Woodrat)
<i>Sylvilagus</i> Avg. VD_{SA}	0.5363 (28) $P=0.0033$	0.4692 (28) $P=0.0118$	0.3930 (28) $P=0.0385$	0.5618 (28) $P=0.0019$	0.6650 (28)
<i>Lepus</i> Avg. VD_{SA}	0.5172 (28) $P=0.0048$	0.3842 (28) $P=0.0436$	0.69 (28)	0.6598 (28)	0.5489 (28) $P=0.0025$

Possible accumulating agent(s) are indicated in parentheses below each site name.

Spearman r , values with sample sizes shown in parentheses, all $P < 0.001$ except where otherwise indicated.

LD/BT estimates tends to show poor correlation in all possible permutations (Table 3). Averaged leporid $VD_{LD/BT}$ estimates compared to averaged marmot LD/BT estimates reveals no significant correlation ($r = -0.05$, $P = 0.07358$, $N = 57$). However, when we compare averaged leporid VD_{SA} with averaged leporid $VD_{LD/BT}$ estimates, the resulting correlation is a slight yet significant and positive relationship ($r = 0.53$, $P < 0.001$, $N = 60$). This suggests the two estimates are measuring similar properties of leporid bones. We believe that the differences might be attributed to a conflation of VD values when LD/BT cross-sectional estimates are used versus an increased variety of VD values when our shape-adjusted estimates are used. For obvious reasons, we believe the latter provide more accurate measures of structural density.

In light of these differences, it is always important to consider the methodologies employed by each study when comparing results. However, as both estimates of VD indicate differences between leporid and marmot structural density assays, we suggest that the primary reason for the dissimilarities lies in some major anatomical differences. Marmots are compact, sturdy and heavy-bodied rodents that construct extensive burrow systems in order to avoid predators and conspecifics, hibernate, sleep and rear young (Barash, 1989). On a daily basis, they are often active above ground for as little as 1–2 h in order to feed (Stokes & Stokes, 1986: 192). In contrast, leporids are highly terrestrial. Rabbits differ from hares in the raising of altricial young. *Sylvilagus* can build nests of shallow, grass and fur-lined depressions (Stokes & Stokes, 1986: 100), whereas *Oryctolagus* can excavate warrens (Thompson & Worden, 1956: 94). However, neither possess forelimbs modified for burrowing. Hares tend to avoid predators through rapid flight on long-striding hind legs, often preferring the sparse vegetation of open areas which enables them to detect approaching danger and still have time to flee. The normal gait of rabbits is the familiar hop. Although freezing is their first response to predator avoidance, rabbits are capable of short bursts of speed into nearby holes or preferred habitats of dense ground cover (Halfpenny & Biesiot, 1986: 47–48; Thompson & Worden, 1956: 94).

Some of these important differences between marmots and leporids are graphically illustrated in Figure 3, which follows Kreutzer's (1992: 285) suggestion to compare the anatomical location of the 10 most-dense and 10 least-dense scan sites. In either taxon, the mid-portion of the calcaneum is relatively high in density, while the sternum is relatively low. Otherwise, the majority of high-density leporid scan sites tends to be concentrated in the hind limbs of the body, particularly the femur and tibia. Marmots have an equal amount of high-density sites in the fore and hind portions, with decidedly dense forelimbs and clavicles. The least-dense scan sites of leporids are located in the forelimbs and ribs, whereas half of the least-dense marmot sites are located in the hind portions of the appendicular skeleton. A pattern of high/low density in hind/fore portions of leporids, and high/low density in fore/hind portions of marmots is further supported when the sample is expanded to the 20 most-dense and 20 least-dense scan sites. This expanded sample includes virtually the entire femur and tibia as high density elements, and more scapular, radial and rib sites as low density areas in leporids. More pelvic, phalangeal and rib sites would be included as high density, with femoral, tibial and pelvic sites as low density areas in the marmot skeleton. If we substitute the leporid $VD_{LD/BT}$ estimates, certain rank orders are rearranged with a few new sites included; however, the basic pattern of high/low density in hind/fore portions remains. We suggest that this pattern is accounted for by the primarily fossorial activities of marmots which place high stress on forelimb elements, in contrast to the terrestrial ricochet locomotion of leporids, which places high stress on hindlimb elements.

Implications for Taphonomic and Actualistic Research

If our leporid structural density assays are both reliable and valid, they raise some interesting issues for assessing bone assemblage formation. In an important paper, Schmitt & Lupo (1995) suggest an innovative approach for assessing differential accumulation histories within

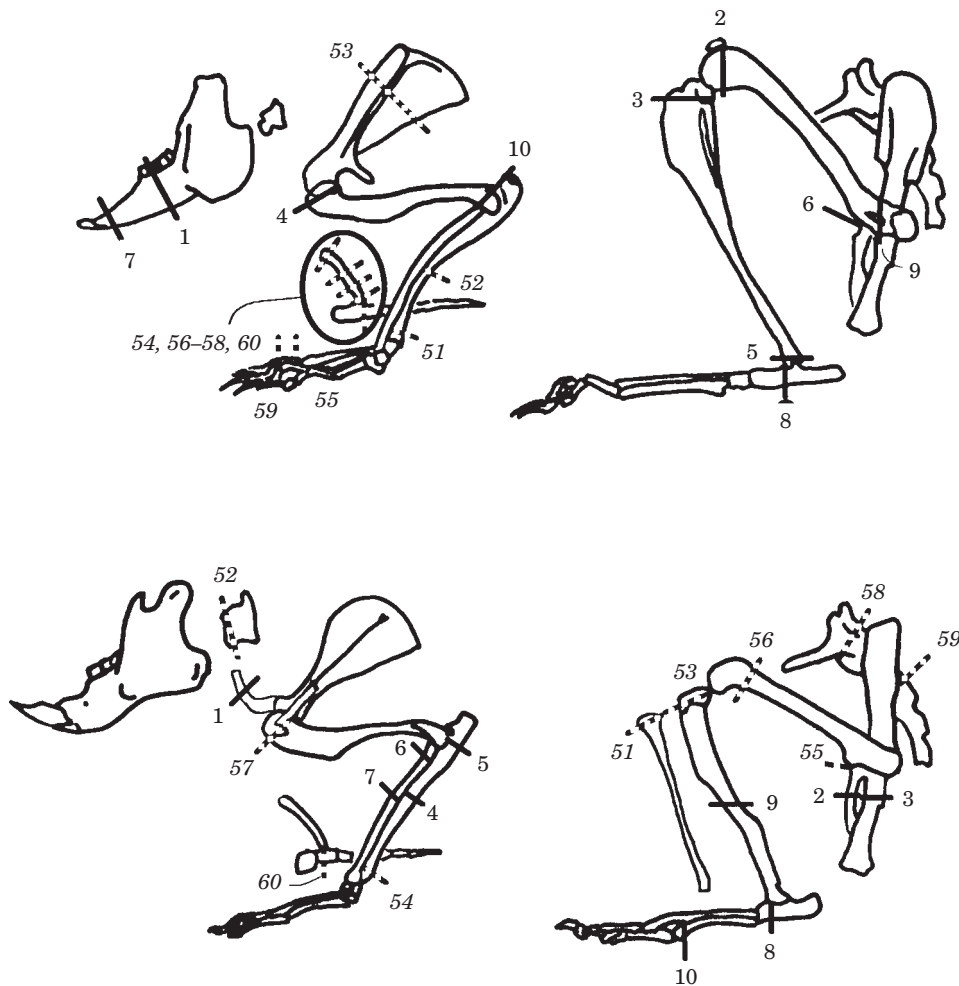


Figure 3. Leporid skeleton (above) and Marmot skeleton (below) illustrating respective locations of the 10-highest (solid lines) and 10-lowest (dashed lines) density scan sites.

multi-agent archaeofaunal assemblages. Their analysis stresses the importance of using multiple lines of evidence, including: bone modification, fragment size and the relation between skeletal representation and structural density. Scatological contributions to deposits in the Rock Shelter site of southwestern Utah were identified on the basis of surface modifications, patterned breakage, intensive fragmentation and density-mediated survivorship characteristic of partial digestion by coyotes. In particular, they demonstrate: (1) a strong, positive correlation between leporid appendicular body segments and structural density for identified leporid scat bone (Schmitt & Lupo, 1995: 501, figure 5); and (2) a non-significant correlation for similar segments identified as human subsistence refuse (Schmitt & Lupo, 1995: 503, figure 6).

As leporid structural density values were unavailable to Schmitt & Lupo's study, they assessed the extent of density-mediated survivorship using structural density values obtained for marmots (Lyman, Houghton & Chambers, 1992). Of course, a problem arises when we

apply the leporid structural density assays to the appendicular body segments identified as scat bone because homologous leporid and marmot values are negatively correlated. Indeed, when the respective leporid values are substituted into their calculations for identified scat bone, the correlation is predictably weak and negative. The strongest negative correlation ($r_s = -0.5126$, $P = 0.1582$) results when we use maximum density values as originally computed in Schmitt & Lupo's (1995) study, and remains weak and negative whether traditional or averaged values are substituted instead (see Lyman, 1994: 257). Similar correlations for identified non-scat bone range from weakly negative to weakly positive. We suggest this to be the case because their study scrutinizes fore and hind limb bone survivorship, or precisely those elements that differ structurally between marmots and leporids.

Our data suggest certain differences in the structural properties of leporid and marmot limb ends. According to our shaped-adjusted (VD_{SA}) estimates, the leporid distal femur is much denser than the

proximal femur. This relation is reversed, with the proximal femur slightly denser than the distal femur in marmots and in our leporid $VD_{LD/BT}$ estimates. The leporid proximal tibia is somewhat denser than the distal tibia, regardless of which VD calculation is used. In marmots, the distal tibia is slightly more dense than the proximal tibia. In the forelimbs, VD_{SA} estimates suggest that the leporid proximal humerus is denser than the distal humerus; however, the relation is reversed when using $VD_{LD/BT}$ estimates, and markedly so in marmots. Either VD estimation suggests that the leporid radius and ulna are relatively low in density. The proximal and distal portions of the radius are essentially similar, whereas the proximal ulna is substantially denser than its very low density distal counterpart. In marmots, these forelimb elements are relatively dense, with the proximal radius denser than the distal radius, and the distal ulna denser than the proximal ulna.

We suggest that the structural differences are best explained by respective differences in animal behavioural adaptations and bone morphology. Marmots are fossorial excavators, whereas leporids are terrestrial locomotors that varyingly rely on flight for escape. Hares avoid predators through high-speed running and leaping. Rabbits escape predation through cryptic behaviour, hopping and the use of constructed burrows. These differences may be reflected in certain higher density hind limb sites amongst *Lepus* and relatively higher density distal ulnae amongst rabbits (Pavao, 1996: 35). Morphologically, the distal ends of the radius, ulna and humerus are relatively slender and gracile in leporids and relatively thick and robust in marmots. The ends comprising the knee joint are pronounced in both taxa, though somewhat more in leporids when compared to their respective proximal and distal counterparts.

If these observations are valid and, as suspected, structural density mediates bone survivorship in predator assemblages (Schmitt & Juell, 1994: 256), then we should see some of these patterns in accumulations known to have been deposited by predators. This is, to some extent, observed when we substitute mean shaped-adjusted (VD_{SA}) leporid estimates for reported bone survivorship in coyote scat assemblages (Schmitt & Juell, 1994: table 4). Here, appendicular and mandibular survivorship is mildly, but positively, correlated with respective density assays ($r_s = 0.4857$, $P = 0.0076$, $N = 29$). Substitution of $VD_{LD/BT}$ estimates result in an essentially similar correlation ($r_s = 0.4994$, $P = 0.0068$, $N = 28$). We suspect that the correlation would be stronger if the entire range of scan sites could be taken into account; however, this is mitigated by the increased difficulty of specifically identifying and accurately quantifying axial specimens, compared to their appendicular counterparts.

Nevertheless, our observations are bolstered by a perusal of leporid accumulations reported in a number

of actualistic studies undertaken primarily in the Great Basin of the western United States (Hockett, 1991, 1993, 1995, 1996; Schmitt, 1995). As these studies are not experimental, the observed survivorship of bone material can not be related precisely to the structure of an original prey population, nor can the exact original state of the accumulated remains as first encountered by the accumulating agent, be known unequivocally. The accumulations can be varyingly attributed to raptor roosting and nesting sites; however, in some cases the exact accumulation mechanism remains uncertain as an array of potential agents, including wood rats, owls, diurnal raptors and carnivores, may have contributed to assemblage deposition. We used data from five sites reported in Hockett (1993: chapter 6) to examine separate Spearman Rank correlations between shaped-adjusted (VD_{SA}) density estimates for *Sylvilagus* and *Lepus*, and respective accumulations for each taxon. At all five sites, correlations between structural density and bone survivorship range from weakly to strongly positive (Table 4). The reason for variable positive correlations in the 10 studied accumulations can be attributed to certain kinds of patterned survivorship. Roost and wood rat accumulations tend to have a particularly high proportionate survivorship of complete hind limb bones. Roosting sites of diurnal raptors appear to be characterized by a greater proportion of hind limb elements, especially from larger-sized leporid prey taxa like jackrabbits (Hockett, 1993, 1995; Schmitt, 1995 and compare with Cruz-Urbe & Klein, 1998: 139). The reported data also list mandibular remains, which are overwhelmingly dominated by the very high density anterior sites (e.g., DN1 and DN2). Also, we note the following patterns of differential survivorship, factoring in the presence of epiphyses: (1) in six of the 10 accumulations, distal femora outnumber proximal femora, and in three of 10, they survive in equal numbers; (2) in only three cases do proximal tibiae outnumber distal tibiae, but in four cases they either match or are fairly close to the number of their distal counterparts; (3) radii are less common in the accumulations, with variable survivorship of either end; and (4) when ulnae are present, they are distinguished by a pronounced survivorship of the proximal end. All these factors appear to be correlated with structural density mediation with the exception of humeri, which when present are more likely to be represented by their distal ends. Of course, while the detection of density-mediated survivorship may tell us something about the ultimate cause of bone survivorship (e.g., patterned destruction ultimately mediated by differential structural density of bone material), it does not identify proximate causation (e.g., patterned destruction proximately mediated by factors like differences in feeding strategies, or digestion, deposition, etc.) in the taphonomic history of assemblage accumulation (Lyman, 1984: 294). This can only be achieved through actualistic study, like the important efforts

undertaken by Hockett (1989, 1991, 1993, 1995, 1996) and Schmitt (1995). Furthermore, the reliability and validity of our density estimations must be corroborated through further experimental studies on similar and related taxa.

Implications for Archaeological Research

If our leporid structural density assays are both reliable and valid, they raise some interesting implications for archaeological research. In his thorough and innovative analysis of a zooarchaeological assemblage from the Bonnell site in southeastern New Mexico, Driver (1995) used the relative abundance of archaeofaunal remains to explore prehistoric utilization of local environments for subsistence resources. In particular, he employed a unique “breakage unit” coding system for skeletal portion recovery (Driver, 1985: 8, 68). Each unit is individually quantified by genus and can be translated relatively well into associated scan sites. The excavated deposits contain evidence of two leporid genera, *Sylvilagus* and *Lepus*. Species-level identification of the leporid taxa was not possible; however, only two species of *Sylvilagus* (*S. audubonii* and *S. floridanus*) are present in the area, as are two species of *Lepus*, one of which, *L. californicus*, is much more common in the region than the other, *L. townsendii* (Driver, 1985: 13). For these reasons, the Bonnell site is an excellent candidate for exploring the archaeological application of our leporid bone density values.

At the time of occupation, the Bonnell site was located on a permanent water source which could support a nearby area of dense vegetation, as compared with the more sparse piñon and juniper vegetation at higher elevations further away from the site (Driver, 1985: 2, 54). The faunal assemblage, consisting of 5826 specimens and representing at least 20 mammalian genera, was excavated from 33 pithouses and *jacal* (mud and straw) rooms. Glencoe phase (AD 1100 to 1450) occupations include sedentary or semi-sedentary habitation sites with a reliance on agriculture (Driver, 1985: 2). Driver (1985: 60) suggests that the procurement of wild animal species was at least partially structured by agricultural scheduling. The hunting of larger taxa, such as deer and antelope, was a group effort requiring travel of some distance away from the habitation site. Smaller animals like cottontails were locally accessible, as they were attracted to human habitation sites and agricultural fields. However, as the preferred open grassland habitat of larger hares is quite unlike the disturbed, brushy habitat characterizing the area immediately surrounding the Bonnell site, their procurement would therefore require travel away from the immediate habitation area. His analysis suggests that this was not practiced to any great extent. Small mammals in general, and lagomorphs in particular, were hunted

opportunisticly in close proximity to habitation sites (Driver, 1985: 59–60).

It should be noted that zooarchaeologists often utilize a “lagomorph index” to gauge the degree of agriculturally-induced environmental modification in appropriate archaeological contexts throughout the desert southwest. This index is a simple ratio which utilizes NISP counts for cottontails and hares to measure the relative proportion of each taxon under the assumption that a relative increase in jackrabbit remains might implicate larger village sites communally hunting these taxa in nearby, open habitats cleared for agriculture. Smaller farmsteads, which could have impacted local environments less profoundly, would in turn be characterized by a higher relative contribution of cottontails (e.g., Szuter & Bayham, 1989; Szuter, 1991).

In either case, the relative proportions of *Lepus* to *Sylvilagus* remains serve as the basis for evaluation. At Bonnell, the recovered *Lepus* subsample (NISP=250, MNI=15) is considerably smaller than the recovered *Sylvilagus* subsample (NISP=1036, MNI=89) (Driver, 1985: 68). Does the relatively low number of recovered *Lepus* remains support an interpretation of opportunistic and local procurement, or might it be attributed to some sort of density-mediated destruction of skeletal portions? We can likely rule out differential transport and introduction of selected skeletal portions to the site by humans, as either taxon is small enough to be easily carried whole by an adult human. Instead, the application of skeletal density assays to smaller taxa likely provides a rough measure of *in situ* destruction within an assemblage. Small animal applications can further act as warning flags for density-mediated destruction, particularly in the absence of available density data for other archaeologically associated taxa.

As Driver (1985: 5) notes, the use of 1/4" aperture screens at Bonnell most likely resulted in the loss of smaller skeletal portions from lagomorphs. In this analysis, we eliminate the smallest leporid bones that were shown experimentally by Shaffer (1992) to pass through 1/4" screen mesh 70% of the time. These bones would include the metacarpals, carpals, metatarsals, tarsals, phalanges, caudal vertebra and patellae of both genera, and the sternum, ribs and astragali of *Sylvilagus*. The extent of density mediation in the Bonnell lagomorph subsample can be conservatively estimated in a number of ways. One way is to aggregate the appropriate scan sites represented in each breakage unit for elements from *Sylvilagus* (Driver, 1985: table A1) and from *Lepus* (Driver, 1985: table A2). The associated density assays for these scan sites in each breakage unit are then statistically compared to the percentage survivorship of each breakage unit, which is calculated in the standard way (Lyman, 1994: 256). The numerator is the frequency of each breakage unit divided by the number of times it occurs in the skeleton, and multiplied by 100. The denominator is

the most frequently occurring breakage unit divided by the number of times it occurs in the skeleton. A comparison of percent survivorship of breakage units in the Bonnell assemblage with averaged VD_{SA} density values indicates a weak and positive correlation ($r_s=0.39$, $P=0.01$, $N=43$) for *Sylvilagus* breakage units, and no correlation for *Lepus* breakage units ($r_s=0.055$, $P=0.7389$, $N=39$). Substituting maximum VD_{SA} density values causes little change, as percent survivorship is still weakly and positively correlated ($r_s=0.33$, $P=0.03$, $N=43$) for *Sylvilagus* breakage units, but not at all correlated for *Lepus* breakage units ($r_s=-0.04$, $P=0.7970$, $N=39$).

A more accurate way to model density mediated survivorship in the two Bonnell lagomorph sub-assemblages is to simply tally the total number of times each scan site occurs in the assemblage. Percent survivorship for each scan site is calculated by substituting scan sites for breakage units in the survivorship equation. The percent survivorship of each scan site can then be compared directly to its corresponding VD_{SA} density value. This simpler derivation offers clearer resolution for an assessment of density mediation as it does not rely on the use of averaged or maximum density assays. However, it does assume that each scan site is completely preserved; an assumption that has to be made for this study, but one that can be easily determined in zooarchaeological analysis. A comparison of percent survivorship of individual scan sites for the Bonnell *Sylvilagus* remains with their corresponding VD_{SA} density values indicates a strong and positive correlation ($r_s=0.625$, $P<0.001$, $N=40$). A comparison of percent survivorship of individual scan sites for the Bonnell *Lepus* remains with their corresponding VD_{SA} density values indicates a relatively weak and positive correlation ($r_s=0.22$, $P=0.1675$, $N=40$).

The application of leporid bone density values to the Bonnell lagomorph archaeofaunal remains supports a density-dependent survivorship of the *Sylvilagus* subassemblage. The density-dependent survivorship of relatively small and portable cottontail skeletons suggests the *in situ* attrition of deposited remains, rather than either the selective introduction of high density or removal of low density *Sylvilagus* fragments from the site. At most, the *Lepus* subassemblage appears to be only weakly correlated with density-dependent survivorship. This suggests that there is no reason to implicate any substantial *in situ* attrition of larger hare remains; therefore, the smaller number of *Lepus* specimens is likely not an artefact of differential preservation. The application of density assays for understanding assemblage survivorship of these two taxa tends to support Driver's conclusion that small animals, including hares, were hunted in the proximity of habitation areas, and likely reflect a garden-hunting, opportunistic approach to the procurement of small game.

Concluding Statement

Since the appearance of Lyman's (1982, 1984) pioneering use of photon absorptiometry to accurately estimate structural bone density, a number of comparable studies for different animal taxa have appeared. We offer these structural density assays of leporid skeletal elements in an attempt to further increase our ability to understand bone density as a mediating factor in assemblage formation. The data further support earlier recommendations that archaeofaunal remains should, whenever possible, be compared with structural density values derived from similar or related taxa (Kreutzer, 1992; Lyman, Houghton & Chambers, 1992). We suggest that some major and understandable anatomical contrasts differentiate comparable density values between leporids and marmots. However, variations in the methods used by different researchers to compute volume density estimations (e.g., Lyman, 1984: 280; Kreutzer, 1992: 284; Elkin & Zanchetta, 1991: 197; Elkin, 1995: 31; Galloway, Willey & Snyder, 1997: 312) should always be considered when assessing the comparability of published assays. Moreover, ideally our data must be corroborated through further experimental studies.

The use of reliable structural density assays is certainly a powerful tool for assessing archaeofaunal assemblage formation (Kreutzer, 1992: 272); however, the accuracy of resolution provided by these tools is only as good as the precision of our analysis. For example, a confounding problem in the study and description of leporid assemblages involves the highly identifiable nature of skeletal portions. In many cases, even the tiniest fragment of some leporid elements can be readily identified, if not to the generic level then certainly to the ordinal level. Often, the identification of a "lagomorph" fragment is used as sufficient evidence to suggest a higher order identification on geographical grounds alone. Although the fragmented greater trochanter of a femur may be sufficient to identify a lagomorph, for taphonomic purposes, the identification of a "proximal femur" can be somewhat imprecise (Lyman, 1994: 268) as it can include three different scan sites with varying structural properties. The taphonomist is faced with the choice between "traditional", maximum, or averaged values (Lyman, 1994: 257), any of which could potentially introduce a certain degree of imprecision. The latter problem can be surmounted by using the scan site as a basic unit for analysis. Driver's (1985) innovative use of breakage units enabled us to increase our resolution of assemblage survivorship at the Bonnell site; however, imprecision remained as fragmentation of scan sites could not be factored into the analysis. We have just completed the preliminary analysis of a large assemblage of leporid remains ($N=14,587$) from highland Ecuador. In this study, we chose to document bone survivorship both in the standard descriptive way and by estimating the percentage representation of each scan site on all

identifiable leporid fragments for which data are available (see Lyman, 1992: 20). In this way, we hope to further increase our resolution of assemblage formation and the potential power provided to us by this highly useful taphonomic tool.

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