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Within-taxon morphological diversity in late-Quaternary *Neotoma* as a paleoenvironmental indicator, Bonneville Basin, Northwestern Utah, USA

R. Lee Lyman*, Michael J. O'Brien

Department of Anthropology, 107 Swallow Hall, University of Missouri-Columbia, Columbia, MO 65211, USA

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Abstract

Ecological data indicate that as the amount of precipitation in an arid areas increases, so too does mammalian taxonomic richness. This correspondence has been found in two late-Quaternary mammalian faunas from Utah, one from Homestead Cave in the Bonneville Basin. We use the remains of two species of woodrat (*Neotoma cinerea* and *Neotoma lepida*) from Homestead Cave to test the hypothesis that as the amount of precipitation in an arid area increases, so too does morphological diversity within individual mammalian taxa. Morphological diversity is measured as corrected coefficients of variation and as richness of size classes of mandibular alveolar lengths. Coefficients of variation for *N. cinerea* are few and coincide with moisture history if temporally successive small samples are lumped together. More abundant coefficients of variation for *N. lepida* coincide only loosely with moisture history, likely because such coefficients measure dispersion but not necessarily other aspects of variation. Richness of size classes of *N. lepida* is high during the early and late Holocene when moisture was high, and lowest during the middle Holocene when climate was most arid.

Keywords: Bonneville Basin; Morphological diversity; *Neotoma* spp.; Percentage-stratigraphy graph; Woodrat

Introduction

It has been found that as the amount of precipitation in an arid area increases, primary productivity increases and so too does the number of mammalian species present (Brown, 1973, 1975; Brown and Gibson, 1993; Meserve and Glanz, 1978; see also Abramsky and Rosenzweig, 1984; Rosenzweig, 1992, 1995; Rosenzweig and Abramsky, 1993). The typical explanation for correlated increases in all three variables is that relative to arid areas with low primary productivity, those with high productivity will support more mammalian taxa because the taxa can be more specialized and still maintain sufficiently large populations to avoid extinction (Brown and Lomolino, 1998, pp. 776–777 and references). The more food energy available, the more it can be divided among different consumers.

It is also known that the amount of intrataxonomic morphological variation reflects the way that a population occupies its niche (Van Valen, 1965). All individuals of the species comprising the population may be generalists, in which case, each uses the entire niche, or each individual is a specialist and exploits only a small portion of the population's entire niche. The former occurs when all individuals are morphologically similar; the latter occurs when individuals are morphologically unique in one or more characters (Roughgarden, 1972). As Roughgarden (1972, p. 684) noted, the "distribution of variability in an ecologically functional trait is relevant to understanding niche width. If a population has much variability in the trait, then it has many kinds of individuals who are taking resources from many different places on the resource axis." The potential adaptive advantage

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* Corresponding author. Fax: +1 573 884 5450.
E-mail address: lymanr@missouri.edu (R.L. Lyman).

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is that "intrapopulation variation in niche occupied permits a greater population size than would otherwise be possible" (Van Valen, 1965, p. 377). Both theoretical considerations and empirical studies indicate that within-taxon morphological variation may correlate positively with primary productivity (Roughgarden, 1972; Van Valen, 1965).

Recent paleoecological research in the arid Bonneville Basin of northern Utah has focused on local paleoenvironmental, floral, and faunal history during the late Quaternary (Broughton, 2000; Broughton et al., 2000; Grayson et al., 1996; Livingston, 2000; Rhode, 2000; Rhode and Madsen, 1995). Grayson (1998, 2000b) found that small-mammal taxonomic richness was relatively high during the moist late Pleistocene and early Holocene, and relatively low during the more arid middle and late Holocene. This relationship between the histories of taxonomic richness and aridity was later documented at another late-Quaternary site 120 km to the south (Schmitt et al., 2002). The amount of precipitation and mammalian taxonomic richness covaried directly in arid areas during the late Quaternary.

We analyzed data derived from some of the faunal remains studied by Grayson (1998, 2000a,b, 2002) but examined morphological variation within a taxon. We tested the following hypothesis: as the amount of precipitation in an arid area increases, so too does morphological diversity within individual mammalian taxa. If the hypothesis is correct, (i) the coefficient of variation for size or shape variables may increase (see below) as precipitation increases and decrease as the amount of precipitation decreases, and (ii) the number of variants of a taxon should increase as precipitation increases and decrease as the amount of precipitation decreases. We do not attempt to determine if the variation we document is genotypic or merely phenotypic, but rather only test our hypothesis regarding the relationship between morphological diversity and precipitation. To perform that test, we examine how one size variable and richness of size classes of the North American woodrat genus *Neotoma* covary with environments during the late Pleistocene and the early, middle, and late Holocene.

Methods and materials

We focus on alveolar lengths of mandibles of woodrat recovered from late Pleistocene and Holocene deposits in Homestead Cave and originally studied and reported by Grayson (1998, 2000a,b, 2002). Homestead Cave is located in the Bonneville Basin of northwestern Utah (see Madsen, 2000 for details), a subregion of the internally drained Great Basin today comprising Nevada and adjacent portions of southeastern Oregon, northeastern and southeastern California, and western Utah. Woodrat mandibles from 13 of 18 strata are discussed here; materials from strata X and XIII–XV are not included as they were not analyzed (Grayson, 2000b), and Stratum XVIII is omitted because of the few *Neotoma* mandibles ($n = 5$) it produced. A total of 1025 woodrat mandibles identified by Grayson as representing two species – desert woodrat (*Neotoma lepida*) and bushy-tailed woodrat (*Neotoma cinerea*) – makes up the sample (Table 1). The mandible's anatomical connection to the skull, its use as an implement for carrying items from which nests are constructed, and its food-processing function all make it likely to be susceptible to natural selection and character displacement (Brown and Wilson, 1956; Eldredge, 1974).

The *Neotoma* mandible sample from Homestead Cave is but a fraction of the total collection of *Neotoma* remains from the site. Most specimens were accumulated by raptors (mostly owls) and woodrats. Both woodrat species represented in the collection tend to forage within 100 m of their nests (Smith, 1997; Verts and Carraway, 2002). Similarly, raptors tend to forage within a few kilometers of their roosts (Andrews, 1990). When interpreting frequencies of faunal remains, the potential for changes in taphonomic processes

Table 1
Frequencies of *Neotoma* spp. mandibles and mandibular alveolar-length 0.04 cm size classes, and mean and range of alveolar length (cm) per chronological period and stratum at Homestead Cave, Utah

Period	^{14}C yr B.P.	Stratum	NISP of Mandibles (Total NISP)				N of size classes	Mean ± SD	Range
			NISP	*N. lepida*	*N. cinerea*	*N.* sp.			
Late Holocene B	1000–1500	XVII	85	85 (2204)	0 (9)	0	4	0.820 ± 0.030	0.74–0.88
		XVI	36	36 (750)	0	0	4	0.820 ± 0.031	0.76–0.88
Late Holocene A	2000–4500	XII	93	92 (2609)	0	1	5	0.828 ± 0.028	0.75–0.90
		XI	57	56 (1482)	0	1	5	0.831 ± 0.028	0.77–0.90
Middle Holocene	5300–8000	IX	130	129 (2976)	0 (1)	1	5	0.838 ± 0.030	0.77–0.90
		VIII	35	34 (985)	0 (5)	1	4	0.842 ± 0.032	0.78–0.92
		VII	58	58 (1627)	0 (4)	0	3	0.835 ± 0.022	0.78–0.88
		VI	114	114 (3445)	0 (5)	0	3	0.837 ± 0.026	0.78–0.88
Early Holocene B	8000–8300	V	28	26 (930)	0 (1)	2	4	0.838 ± 0.033	0.78–0.90
		IV	195	183 (5164)	11 (242)	1	8	0.845 ± 0.045	0.76–1.03
Early Holocene A	8300–10,200	III	21	11 (345)	9 (306)	1	8	0.894 ± 0.085	0.76–1.02
		II	69	12 (280)	54 (1508)	3	8	0.957 ± 0.066	0.79–1.06
Late Pleistocene	10,200–11,300	I	104	0 (41)	101 (2577)	3	5	1.010 ± 0.038	0.92–1.09

responsible for those remains must be considered (Lyman, 1994). There is no evidence among any of the Homestead Cave faunal remains that changes in accumulation, deposition, or preservation took place (Broughton, 2000; Grayson, 2000b; Livingston, 2000).

The bushy-tailed woodrat has a deep anterolingual reentrant angle on the upper first molar, whereas the desert woodrat has a shallow anterolingual reentrant angle on that tooth (Grayson, 1983; Hall, 1981; Harris, 1984). Bushy-tailed woodrats consume a wider variety of fibrous plant tissue than desert woodrats, so the former taxon may require more enamel surface area to process the fiber (Grayson, 1999, 2000b). Zakrzewski (1993, p. 403), for example, noted that the larger "anterolingual fold on the [upper] first molars increases the enamel shearing surface in a small area where food first enters the mouth." Many woodrat mandibles recovered from sites in the western United States are edentulate, precluding use of dental traits and forcing reliance on size for identification of prehistoric specimens to the species level (e.g., Grayson, 1983; Harris, 1984; Rensberger and Barnosky, 1993).

Modern desert woodrats have mandibular alveolar lengths that are smaller than, and do not overlap, those of bushy-tailed woodrats (Grayson, 1983, 1988). Modern comparative specimens of known taxonomy indicate that mandibles with alveolar lengths < 0.90 cm represent the desert woodrat, whereas those with alveolar lengths > 0.93 cm represent bushy-tailed woodrats (Grayson, 1983, p. 114). Those with alveolar lengths of 0.90–0.93 cm cannot be reliably assigned to one or the other species (Grayson, personal communication 2000). When Grayson measured specimens, he excluded modern and prehistoric mandibles of juvenile individuals such as those in which the three molars were not fully erupted. Grayson (2000b) compared the taxonomic identifications of specimens based on morphology of the upper first molar with identifications based on the occlusal length of that tooth and found an error rate of 1% over a total collection of mandibles from Homestead Cave. This suggests that alveolar lengths provide a valid diagnostic of the two species of *Neotoma* under consideration.

Given that size is used to identify species, some degree of stability in intrataxonomic size is built into our analysis; all specimens identified as a particular species will fall within the size range used to identify that species. The mean size and range could, however, vary over time, as could variation in size or the number of size classes represented within a taxon. We use two methods to monitor variation in alveolar length displayed by *Neotoma* mandibles. One is the corrected coefficient of variation, calculated as

$$\text{corrected } CV = (1 + [1/(4\text{n})])([\text{SD}/\text{mean}]100)$$

where *n* is the sample size, SD is the standard deviation, and mean is the sample mean. We use the corrected CV instead of the simple CV because of the wide variation in sample size per stratum (number of measured mandibles per stratum ranges from 20 to 194). Without this correction, small samples tend to underestimate variation (Sokal and Rohlf, 1995, pp. 57–59). The corrected CV provides an indication of variation in a sample, but it does not tell us directly about the richness of morphological variants in the taxon nor does it provide an intuitively obvious indication of how variation is distributed within a population. As Simpson et al. (1960, p. 90) observed, the CV "is in every case a good measure of dispersion, but relative dispersion is not always a good measure of variability." The CV (corrected or not) is a sufficient but not a necessary test implication of the hypothesis that intrataxonomic variation should increase as moisture increases. A second measure of variation is thus called for.

The other method we use to monitor variation in alveolar length involves nine size classes with increments of 0.04 cm each. These classes represent a compromise between having a sufficient number of size classes to avoid problems with interpreting closed arrays ($\sum = 100\%$) when few classes are used and having sufficient specimens within each size class to avoid problems of small samples per class. This set of size classes allows division of the total size continuum into four classes smaller than and four classes larger than the nondiagnostic size class of 0.90–0.93 cm. Larger size-class increments of 0.05 cm and 0.06 cm do not allow division into equal numbers of size classes within each species and display little variation in the number of represented classes over time. Smaller size classes of 0.02 cm, 0.03 cm, and 0.04 cm increments all produce similar results in terms of changes in richness over time (Fig. 1), but the 0.03 cm class encounters the problem of how to deal with the nondiagnostic 0.90–0.93 size, and the 0.02 cm class has so many classes as to not reveal robust patterns in the percentage-stratigraphy graph (see below) because of idiosyncratic representation of size classes. The 0.04 cm size class increments we use are arbitrary and represent analytical decisions based on practical concerns.

We use a percentage-stratigraphy graph (Lyman et al., 1998) to examine intraspecific variation in represented size classes. This graph comprises a set of columns of horizontal bars of various widths centered and stacked one atop another. Each column represents a unique class (in this case, size class), and thus the number of columns in a row with members is the richness of classes. Each row of bars represents a stratigraphically unique assemblage. Bar width signifies the relative (proportional) abundance of a size class within a set of stratigraphically associated specimens comprising multiple size classes. Rates of change can be determined based on the temporal scale represented by the vertical axis. A percentage-stratigraphy graph simultaneously shows the richness of classes (however defined) and the relative frequency of each class over time.

Frequencies of *Neotoma* mandibles are given as the number of identified specimens (NISP). We use ordinal-scale statistics in analyses of prehistoric specimens because

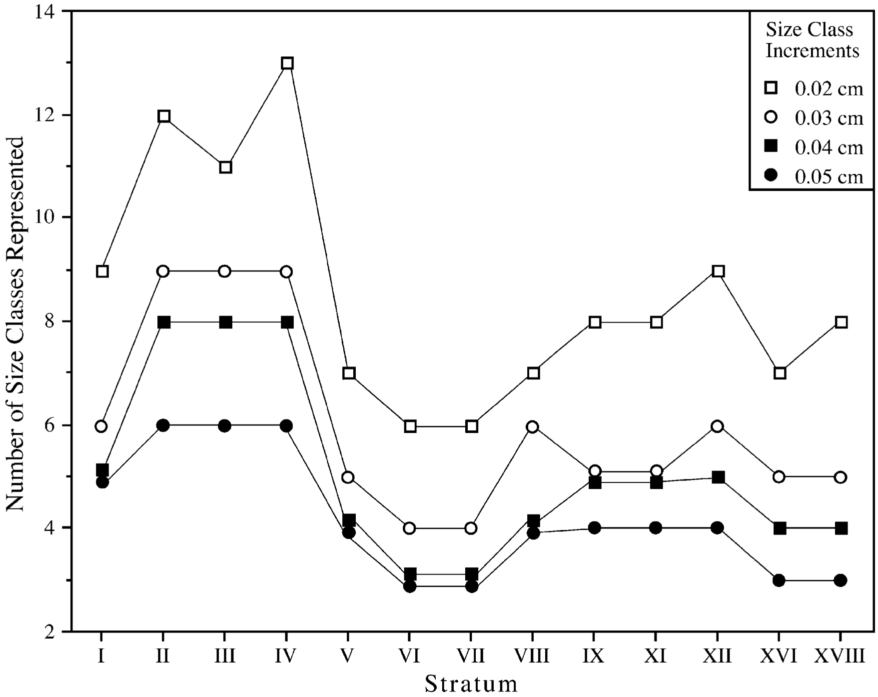

Figure 1. Richness of *Neotoma* mandibular alveolar length size classes per stratum for 0.02 cm, 0.03 cm, 0.04 cm, and 0.05 cm size classes.

NISP values typically are at best ordinal scale (Grayson, 1984). Ordinal-scale statistics also circumvent the problem of the interdependence of left and right mandibles coming from the same animal. All ages are reported as uncalibrated ^{14}C yr B.P.

Natural history of woodrats

Today, the desert woodrat is found in low elevation, desert-shrub habitats of much of the Great Basin and is aptly named for its inhabiting desert and semi-desert environments (Verts and Carraway, 2002). It is found no farther north than southern Idaho/Oregon and is continuously distributed southward through Nevada and western Utah into southeastern California and along the entire length of Baja California. There is fossil evidence that sometime during the Pleistocene the desert woodrat occurred in southern Washington state more than 200 km north of its modern northernmost occurrence (Rensberger and Barnosky, 1993). Estimates of body mass and taxonomy based on the diameter of prehistoric fecal pellets recovered from sites in southcentral Idaho suggest that the desert woodrat may have invaded low elevation areas 150 km north of its modern range during the climatically warm-dry middle Holocene (Smith and Betancourt, 2003). Many linear dimensions of the desert woodrat are longest in southern populations and shortest in northern populations (Verts and Carraway, 2002). In contrast, body mass of desert woodrats displays an east-west gradient; large individuals are found along the California coast and small individuals in interior deserts (Smith and Betancourt, 2003). The largest desert woodrats are found where food resources are abundant, and the smallest individuals are found where resources are scarce (MacMillen, 1999).

The bushy-tailed woodrat is the most boreal of the several species within the genus. It is found as far east as the western half of North and South Dakota, and it ranges from the mountains of northern Arizona and New Mexico into the Northwest Territories (Smith, 1997). It cannot withstand high ambient temperatures, especially those of the summer (Smith and Betancourt, 1998; Smith et al., 1995), perhaps because of its thick pelage (Smith, 1997). Pleistocene age remains of bushy-tailed woodrats have been found at elevations lower than where this animal occurs at present and at latitudes south of its modern range (e.g., Harris, 1984). Body mass of modern bushy-tailed woodrats exemplifies Bergmann's rule: large individuals are found in cooler climates and smaller individuals are found in warmer climates (Brown and Lee, 1969). Some data for the late Quaternary indicate that bushy-tailed woodrats were largest when temperatures were cool and smallest when temperatures were warm (Smith and Betancourt, 1998, 2003; Smith et al., 1995, 1998).

The two species tend to occupy different habitats and elevations. Desert woodrats are typically found in low-elevation desert-shrub habitats and bushy-tailed woodrats in higher-elevation woodlands, though the elevational range of both species will vary with latitude. In some portions of their ranges, the two species are sympatric. In such cases the desert woodrat, the smaller of the two species, is subordinate to the larger bushy-tailed woodrat (Smith and

Betancourt, 2003). Both species are represented in all but strata I, XI, XII, and XVI at Homestead Cave (not always by mandibles), so character displacement may be a problem. We are unaware, however, of any documentation of such when the two species of concern are sympatric, so we do not consider this variable further here.

Paleoenvironmental background

Paleobotanical data from the Bonneville Basin and adjacent areas suggest that both the terminal Pleistocene (ca. 15,000 to 10,000 ^{14}C yr B.P.) and early Holocene (10,000 to 7500 ^{14}C yr B.P.) were wetter and cooler than today (Rhode and Madsen, 1995). Paleomammalogical data also suggest lower than modern temperatures coincident with greater than modern moisture at that time (Grayson, 1998, 2002; Smith and Betancourt, 1998, 2003; Smith et al., 1995). The late Pleistocene was cooler and moister than the early Holocene, and it is likely that early Holocene B was warmer and drier than the preceding early Holocene A (Table 1). During the middle Holocene, usually thought to span 7500 to 4500 ^{14}C yr B.P., paleobotanical data suggest precipitation decreased coincident with higher temperatures (Wigand and Rhode, 2002). Again, paleomammalogical data align well with this paleoenvironmental scenario (Grayson, 1998, 2002). The first half of the middle Holocene was marked by far warmer temperatures and greater aridity than what preceded or succeeded it. Some evidence indicates moisture increased beginning about 5500 ^{14}C yr B.P. (Rhode, 2000; Wigand and Rhode, 2002). Late Holocene paleobotanical data indicate cooler and moister conditions after 4500 ^{14}C yr B.P. than during the preceding period, but they also indicate that the last 4500 ^{14}C yr or so were, on average, not as cool and moist as the terminal Pleistocene and earliest Holocene (Wigand and Rhode, 2002). The prehistoric record of mammals also suggests a return to cool, moist conditions during the late Holocene (e.g., Grayson and Madsen, 2000). After about 2000 ^{14}C yr B.P., during late Holocene B, conditions were a bit drier and warmer than during late Holocene A (Rhode, 2000). The order of strata from greatest to least moisture is: stratum I, strata II and III, strata IV and V, strata XI and XII, strata XVI and XVII, strata VIII and IX, and strata VI and VIII.

Results

Mandibles make up 3–5% of *Neotoma* remains per stratum, and the abundance of mandibles per stratum is highly correlated with the total NISP of *Neotoma* per stratum (Spearman's *rho* = 0.978, $P < 0.0001$). Frequencies of mandibles are thus good measures of the abundances of woodrat remains throughout the stratigraphic sequence. Both the taxonomically distinctive upper first molar (Grayson, 2000b) and the mandibular alveolar length data show turnover in species of woodrat (Table 1). What does the morphological diversity data show? Only four strata (I–IV) produced measurable *N. cinerea* mandibles; all were deposited during the late Pleistocene and early Holocene. During that time, moisture decreased more or less consistently. The corrected CV values for *N. cinerea* decrease from stratum I (3.771) to stratum II (3.260), to stratum III (2.724), but then increase with stratum IV (3.062). The samples for strata III and IV are quite small (NISP = 9 and 11, respectively), so they may not be representative of the bushy-tailed-woodrat population present at the time. If the samples from strata III and IV are lumped, the corrected CV (2.869) is less than that for stratum II, and thus the implication of our hypothesis is met.

There is no correspondence between the magnitude of a stratum-specific corrected CV for *N. lepida* mandibles and climatic moisture when a stratum was deposited (Table 2). Sometimes a CV is high when moisture level was high (e.g., strata III and V), and other times a CV is high when

Table 2
Descriptive statistics and corrected coefficients of variation for *Neotoma lepida* and *N. cinerea* mandibles

Stratum	*Neotoma lepida*		*Neotoma cinerea*		*Neotoma* spp.
	Mean ± SD	Corrected CV	Mean ± SD	Corrected CV	Corrected CV
XVII	0.820 ± 0.030	3.669	–	–	3.669
XVI	0.820 ± 0.031	3.807	–	–	3.807
XII	0.827 ± 0.027	3.274	–	–	3.391
XI	0.830 ± 0.027	3.268	–	–	3.384
IX	0.838 ± 0.029	3.467	–	–	3.587
VIII	0.840 ± 0.029	3.478	–	–	3.827
VII	0.835 ± 0.022	2.646	–	–	2.646
VI	0.837 ± 0.026	3.113	–	–	3.113
V	0.833 ± 0.029	3.512	–	–	3.973
IV	0.835 ± 0.025	2.998	0.994 ± 0.030	3.062	5.332
III	0.819 ± 0.030	3.746	0.981 ± 0.026	2.724	9.621
II	0.831 ± 0.023	2.825	0.986 ± 0.032	3.260	6.921
I	–	–	1.010 ± 0.038	3.771	–

moisture level was low (e.g., strata XVI and XVII). The implication of our hypothesis that a CV should be high when moisture level (and thus primary productivity) is high is not met by the corrected CVs for *N. lepida*. We believe this is because the corrected CVs for various stratum-specific samples of mandibles need not be good measures of variability for any of several reasons (Simpson et al., 1960).

If local *Neotoma* responded to the decrease in moisture that occurred after the early Holocene in a manner like that displayed by small-mammal taxa in general at Homestead Cave (Grayson, 1998, 2000b) and elsewhere (Schmitt et al., 2002), then the early strata should contain more size classes than the later strata. Previous research shows that larger samples tend to contain more categories of phenomena, whether taxa, skeletal elements, or size classes (Grayson, 1984, 1998, 2000b). Considering all strata and both species, the number of 0.04 cm size classes represented per stratum is not a function of the number of mandibles recovered from the stratum (*rho* = 0.131, $P = 0.67$). The mean number of size classes represented in strata I–V (= 6.60 ± 1.95) is significantly larger than that in strata VI–XVII (= 4.12 ± 0.83; Student's $t = 3.214$, $P = 0.008$). This is, however, not a robust test of our hypothesis that amount of moisture in arid areas influences morphological diversity because two species are represented in strata II, III, and IV, and only one in later strata, and the two are of different sizes. Not surprisingly, then, the greatest richness of size classes occurs when species richness is highest. If only *N. lepida* mandibles are considered, the lowest observed values of size-class richness occur in strata VI–VIII (three or four size classes), which were deposited during the warmest, driest period in the stratigraphic sequence. Richness increases in stratum IX during the second half of the middle Holocene, when it was more moist. It stays high during the first half of the late Holocene (strata XI and XII), when it was moister still, and then drops in the second half, coincident with greater aridity. Richness of size classes is also high in the early Holocene strata III–V, when climate was relatively moist. The low richness in stratum II is likely the result of the small sample of *N. lepida* mandibles from this stratum and the morphological bottleneck of a small population. These observations conform to the hypothesis that richness of types of a taxon in an arid area will correlate positively with amount of moisture.

Stratum-specific relative frequencies of specimens per size class per species are shown in Figure 2. Samples in strata VI and VII are virtually identical with respect to mean and range of length (Table 1), but Figure 2 indicates that (1) there are more specimens near the center (size class 0.82–0.85) of the Stratum VII frequency distribution (57%) than in Stratum VI (49%) and (2) fewer individuals are found in both extremes of the range (both the 0.78–0.81 class and the 0.86–0.89 class decrease 4% from Stratum VI to Stratum VII). This shift in frequencies is reflected by the corrected CV for the Stratum VII assemblage being lower than that for the Stratum VI assemblage (Table 2). The frequency distributions of size classes in strata VI and VII seem to reflect a period of low primary productivity bounded by periods of greater moisture, higher productivity, and greater morphological diversity of desert woodrats.

Discussion

It is a basic assumption of paleozoology that changes in relative taxonomic abundances and geographic distributions of taxa are "second order responses to climate changes and are probably directly influenced by first order responses,

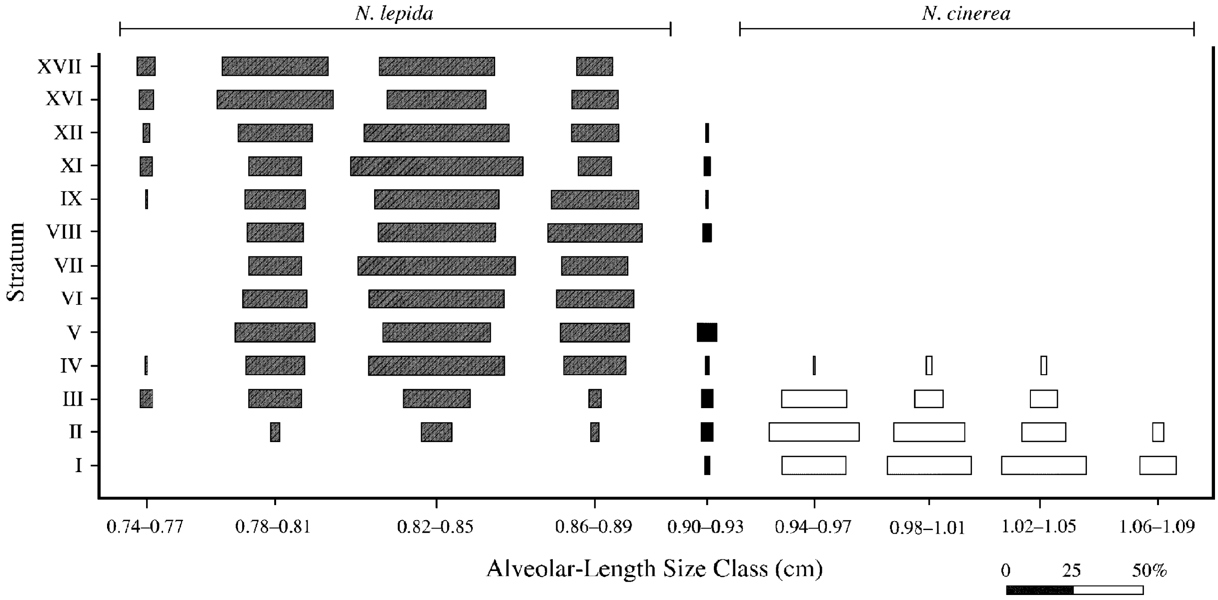

Figure 2. Percentage-stratigraphy graph of nine size classes (of 0.04 cm each) of *Neotoma* alveolar lengths for mandibles from Homestead Cave, Utah. Bars represent percentages and sum to 100% for each stratum.

that is, floral distributions" (Graham, 1976, p. 347). However, the caution sometimes is raised that climatic change is "an intuitive but far from proven stimulus" of change in the taxa comprising a faunal community (Barnosky, 1994, p. 173). Recent actualistic work with samples of faunal remains extracted from modern owl pellets suggests that changes in the taxa represented by such remains sometimes do, in fact, correlate with instances of vegetation change (Lyman and Lyman, 2003).

One of the benefits of working with remains of Quaternary organisms is that very often there are multiple, independent lines of paleoecological evidence for the area and time span under study. These sets of data can be compared, and if all suggest the same cause of faunal change, then confidence in that particular cause can be great. Other benefits include the facts that (1) samples of remains are often much larger than those available for more remote time periods; (2) temporal resolution is often of a very fine scale given available radiometric chronometers; and (3) the ecologies of modern representatives of the taxa represented by the prehistoric remains are often well known (Barnosky, 1987, 1993, 1994). These benefits are particularly critical to analyses focused on fine-scale evolutionary processes such as intrataxonomic plasticity and microevolutionary change (e.g., Barnosky, 1994; Hadly, 1997; Hadly et al., 1998).

Adaptively plastic species will respond ecophenotypically to climatic changes of relatively small magnitude, whereas if the magnitude of climatic changes is sufficiently large so as to exceed the limits of plasticity of the taxon, then taxonomic change will occur (not necessarily precluding intrataxonomic ecophenotypic change). The late-Quaternary mammalian faunal record of North America indicates that the change from terminal Pleistocene to early Holocene climates prompted local extirpations, biogeographic adjustments, and shifts in relative taxonomic abundances, as did the change from the early to the middle Holocene. Some intrataxonomic change also occurred during the terminal Pleistocene (Barnosky, 1990, 1993) and during the Holocene (e.g., Hadly, 1997; Purdue, 1980). Failure to find correlations between intrataxonomic changes in morphometry and evidence of climatic change suggests some of the morphometric changes may signify drift, whereas detected correlations reflect either in situ evolution of a population or replacement of a local population with a nonlocal immigrant population (Barnosky, 1994; Koch, 1986).

The remains of the two *Neotoma* species from Homestead Cave span the terminal Pleistocene and the entire Holocene, and taxonomic abundances indicate the local extirpation of *N. cinerea* and increased relative abundances of *N. lepida* (Grayson, 2000b, 2002). Sometimes prior to 1000 ^{14}C yr B.P., *N. cinerea* recolonized the area around Homestead Cave (Grayson and Madsen, 2000), where it is found today (Grayson et al., 1996). This recolonization, however, is not reflected by the mandibles of the genus. Some of the temporal variation in mandibular alveolar length can be attributed to genetic change in the form of change from one species to another. What appears on other bases to be intraspecific change in size of desert woodrat (Fig. 2) might be attributed to ecophenotypic plasticity or drift.

Conclusion

Paleozoologists have traditionally studied the presence–absence and relative abundances of Linnaean taxa. This makes sense because biologists typically study the ecology of exactly these kinds of taxonomic units, and the knowledge they generate is used by paleozoologists to interpret the animal remains they study. Ecophenotypic responses of taxa to environmental change have also long been studied by paleozoologists interested in assessing past environments. The tendency has been to study each aspect of faunal change separately. Both morphological diversity and taxonomic diversity can, however, be shown simultaneously in graphs like the one shown in Figure 2. Such graphs allow us to track both aspects of faunal change and how they covary over time.

The richness of mammalian species is relatively high during the late Pleistocene–early Holocene and relatively low during the middle and late Holocene at Homestead Cave, just as various modern data would lead us to predict. Morphological diversity in the genus *Neotoma* measured as the richness of size classes and as the corrected coefficient of variation of mandibular alveolar lengths is also relatively large during the late Pleistocene and early Holocene, but this is a result including two congeneric species of disparate size. Considering the desert woodrat alone, on the one hand, the corrected coefficient of variation shows no pattern of change that corresponds with climatic history. On the other hand, the number of size classes is large when climate is moist and smaller when climate is drier. Our hypothesis that morphological diversity within mammalian taxa in an arid area is correlated positively with amount of precipitation receives confirmation from the richness of size classes but not from corrected coefficients of variation. This underscores the point that it may be necessary to use multiple measures of intrataxonomic variation because it is a multidimensional property (e.g., Foote, 1997). Determination of the paleoecological significance of our observations regarding changes in morphological variation in *Neotoma* requires data on such variation among modern woodrats collected from areas with well-known moisture regimes.

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